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STRATIGRAPHIC SIGNIFICANCE OF MISSISSIPPIAN ENDOTHYROID FORAMINIFERA

By EDWARD J. ZELLER [1]

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ABSTRACT

The use of *Endothyra* as an index fossil of Meramecian deposits, especially of the Salem limestone, is not new. However, extensive studies of Mississippian limestones from lower Kinderhookian to Chesteran have revealed the presence of this group of Foraminifera throughout the section. Examination of some of these limestones from which *Endothyra* had not been reported previously has yielded them in great abundance. They first appear in Upper Devonian strata, become fairly abundant in Kinderhookian and Osagian deposits, and attain maximum development, both in size and abundance, in Meramecian limestones, then decline somewhat in the Chesteran. *Endothyra,* as previously recognized, is found to contain forms that should be excluded from the genus.

Secondary deposits within the shell, as well as gross form and mode of coiling of the shell, are found to have definite stratigraphic importance. Besides the stage of evolution, the ratio of planispiral forms to those coiled in a three-dimensional spiral pattern gives further aid in zone differentiation. The trends in phylogeny can be followed throughout the Mississippian into rocks of early Pennsylvanian age. The exact relationship of endothyroids and fusulinids has been a subject of long controversy. Evidence seems to indicate that they both descended from a common ancestor. The endothyroids which coil in the three-dimensional spiral pattern branch from the ancestral stem lower in the section than the planispiral forms and the fusulinids develop at a still higher position.

1. Department of Geology, University of Wisconsin; formerly Assistant Instructor of Geology, University of Kansas.

INTRODUCTION

The genus *Endothyra* has been treated frequently in paleontological literature without adequate attention to the original reference. In a few reports some stratigraphic importance was attributed to the species described, but no zonation of any part of the Carboniferous section was attempted on the basis of these foraminifers. Furthermore, many forms assigned to the genus are so different from the type figure and original description that they are judged to be excluded properly from *Endothyra*. All together, these forms comprise a group which contains at least two genera. The term "endothyroid," which has been applied to the group, indicates similarity in wall structure and apertures, but there are differences in the number and arrangement of the septa and in secondary deposits.

The appearance of the most primitive endothyroid in Devonian rocks, followed by rapid evolutionary development and expanded size of forms in Kinderhookian (Lower Mississippian) strata and reduced size in Osagian (Lower Mississippian) formations are of note from a straigraphic standpoint. The extreme increase in size and marked change in morphology, especially in the mode of coiling, are of special significance in Upper Mississippian rocks of Meramecian age. The existence of a marked unconformity between Osagian and Meramecian deposits in the Mississippi Valley area is reflected in the sudden change of appearance of the entire group of endothyroids.

The continuation of the endothyroid group into Upper Mississippian rocks of Chesterian age is marked by further development of the secondary deposits and a reduction in size. The same general trend continues in Pennsylvanian beds, with a slight increase in size and a tendency to become partially evolute. The upper limit of the range of endothyroid foraminifers is not definitely known. Some authors have placed the limit at the Pennsylvanian-Permian boundary whereas others have described forms from the Triassic which they assign to *Endothyra*.

Since the completion of the manuscript for this paper, work on endothyroid faunas from the Brazer and Madison formations of the Wasatch Mountains east of Logan, Utah, has been started. This work has revealed several significant facts. The endothyroid faunas of the lower and middle portions of the Brazer limestones respectively show strong resemblance to assemblages from the Salem and Ste. Genevieve limestones (Meramecian) of the Mississippi Valley region. The upper 300 feet of the Brazer contains forms which show a strong, though possibly superficial, resemblance to those in Chesterian strata of southern Illinois. It will be necessary to study the Chesterian endothyroids from the type region more fully before this correlation can be established firmly.

Endothyroids from the Madison limestone which underlies the Brazer resemble no fauna thus far examined from any portion of the Mississippian in the type area. It is possible that the forms from the Madison may belong to a different faunal province from those of the type Mississippian.

Both *Endothyra* and forms referred to a new genus, *Plectogyra,* described in this paper, are present in abundance in the Madison. Some forms, belonging to both, have well-developed secondary deposits on the floor of the chambers, whereas others which show the same general characteristics of coiling are free from such deposits. Size relationships are also indefinite, for in some beds large forms are found in association with small ones.

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PREVIOUS WORK

The first reference to the genus *Endothyra* appeared in *The Elements of Fossil Conchology* by Thomas Brown in 1843. It seems that Brown either obtained permission to use an unpublished manuscript of John Phillips or that he saw such a manuscript in the possession of Phillips and assumed that it had been published, because he cites the genus as *Endothyra* Phillips. In a recent paper (Scott, Zeller & Zeller, 1947, p. 557), it was stated that according to the Rules of Nomenclature, Phillips should be considered the true author of the genus. Further consideration of decisions on taxonomy rendered by the Internaional Zoölogical Commission, however, indicates that in spite of the fact that Brown attributed the genus to Phillips, it must be considered as Brown's, since Phillips' description was not published until three years later.

The problem as to what constitutes the genus *Endothyra* is difficult to determine since the type specimen of *Endothyra bowmani* has been lost. After Brown's original publication and designation of the type specimen, the collection belonging to Phillips, which included the holotype, is reported to have been stolen and supposedly it is destroyed. If this is true, there is no possibility of recovering the type specimen.

The description of the holotype is so vague and incomplete that in some respects several interpretations are possible. Since 1843, the name *Endothyra* has come to have a broad meaning which does not follow the original description. Most authors include in the genus a number of forms which are not planispirally coiled and which show other characteristics which do not conform to the original reference.

REASONS FOR ESTABLISHING A NEW GENUS

In working with the group of foraminifers which has been included in *Endothyra*, such important differences between some of the forms have been noted that it is judged needful to distinguish a new genus. A photographic reproduction of the original figure of *Endothyra bowmani* is shown in Plate 3, figure 5. This figure obviously represents a planispiral form, but undoubtedly, also, it is an artist's drawing which may be inaccurate. The text which accompanies the figure does not state the exact form of the shell or the mode of coiling. It is quoted as follows (BROWN, 1843):

> Genus XI.—ENDOTHYRA—Phillips
>
> *Generic Character.*—Shell involute, discoidal, internally concamorated, the chambers communicating by a large perforation; the septa arranged in stellated order; their emarginations on the inner part of their disk; destitute of any shelly siphuncle. Form of the septal edge unknown. Size, one-fiftieth of an inch. *Endothyra Bowmani.* Plate VI., fig. 2. Found in the Mountain limestone of Westmoreland.

While several interpretations of these statements are possible, it seems logical to assume that what is being described in the text is similar to, if not exactly like, the figure shown in the plate. The statements that the septa are arranged in stellated order and that the shape of the shell is discoidal indicate that the form is planispiral in coiling. This is borne out by the figure.

A large percentage of the forms included in the genus *Endothyra* as cited in the literature up to this time, are not planispiral and they do not agree with the type description in other characteristics. The coiling is not in a plane, and in these twisted forms, the attitude of the septa and the angle at which they curve away from the outer wall differs from that in planispiral shells like the original *Endothyra*. As a result of these differences, it seems desirable to establish a new genus to include the endothyroid forms which are not planispiral. This is named *Plectogyra*.

DESCRIPTION OF THE NEW GENUS **PLECTOGYRA**

The new genus is founded on *Plectogyra plectogyra*, new species, from the St. Louis limestone, Meramecian (Mississippian), at St. Louis, Mo., as genotype.

The shell is discoidal and probably umbilicate on one side only. It is involute, having a broadly rounded keel, chambers swollen between the sutures, and the apertural face asymmetrical during most stages of growth. The aperture, which is low and slitlike, is situated at the center of the base of the apertural face and reflects its asymmetry. A tunnel or low passage extends back through the entire coil to the proloculus and is secondarily enlarged by resorption, the height of the tunnel commonly being a little greater than the height of the aperture.

The coiling is particularly distinctive in being logarithmic in character, but the spiral is twisted along an axis so that a three-dimensional spiral is produced. The amount of twisting which takes place during generation of the spiral is called the degree of angular or rotational distortion. The total rotational angle, defined as the sum of all of the angles between each of the half-volution tangent planes, observed in the genotype species, is found to be intermediate between that of strongly distorted forms in Chesterian beds and that of less distorted forms of Kinderhookian rocks. This type of spiral has been defined (SCOTT, ZELLER & ZELLER, 1947, p. 558) as endothyroid, but now it seems desirable to call it a plectogryoid spiral.

The wall of *Plectogyra* is calcareous. There are two distinct layers, a less distinct third layer, and well-developed secondary deposits. The outer wall appears as a thin, dark line in thin sections, resembling the tectum of fusulinids. This outer wall undoubtedly contains more organic material than do any of the other layers of the wall. The major portion of the shell wall is made up of material which probably corresponds to the tectorium of fusulinids.

The proloculus of *Plectogyra plectogyra* is about 80 microns in diameter, but it is not perfectly shown by the holotype. The thickness of the wall in the last volution averages about 60 microns. There are nine septa in the last volution, and it is the only whorl in which all of the septa are visible. The maximum diameter of the shell is about 540 microns. The secondary deposits are well-developed and appear as rounded nodes of amorphous calcite on the floor of the chambers directly behind the septal ends. The secondary deposits are invariably best developed in the last-formed chamber, directly behind the aperture, and they are partly resorbed in the older chambers. The deposit in the terminal chamber probably forms a ridge behind the aperture, producing a vestibule.

The locality from which the type specimen of the genotype species was collected in an abandoned quarry about six blocks from the Mississippi River bluffs which form the type section of the St. Louis limestone in the southeastern part of the city of St. Louis, Missouri. The specimen was taken from a bed located 4 feet above a prominent disconformable break about 20 feet above the bottom of the quarry. The zone itself is a 26-inch bed of dense, nodular, gray limestone which shows greenish-gray shale partings between the beds and contains numerous fragments of *Melonechinus*. A photomicrograph of the holotype is shown in Plate 3, figure 2.

GENERALIZED CHARACTERS OF PLECTOGYRA

Characteristics of the genus *Plectogyra* which apply to its specific variations will be discussed here. Most significant of these is the nature of coiling. Inasmuch as the genus *Endothyra* has been defined to contain planispiral shells, *Plectogyra* is differentiated from it by the nature of its coil. The plectogyroid spiral is invariably three-dimensional and shows the axis of crossing of the planes which are tangent to the curve of each half-volution. No chambered foraminifer which conforms to other characteristics of the genus can be correctly classified as *Plectogyra* if the coiling of the shell is two-dimensional.

Also of prime importance in defining the genus is the character of the shell. It is chambered. It is generally involute, but some evolute forms are known. An aperture occurs at the base of the antetheca. It is low and slitlike, conforming to the asymmetry of the antetheca. Secondary deposits may be present within the shell but all forms do not show these deposits; in some, they are much more prominently developed than in others. These deposits may take the form of nodes or ridges on the floor of the chambers or they may appear as sharp, anteriorly-directed hooks. In some forms, the mounds, nodes, or hooks may fuse along the floor of the chambers so as to form a massive layer of calcite which in some shells reflects the nodes or hooks as lumps on the upper surface. The maximum development of the secondary deposits occurs when the hooks or nodes fuse so completely that a nearly smooth solid layer is deposited on the floor of the chambers. Another less commonly seen type of secondary deposit comprises secondary calcite on the anterior or posterior side of the septum at its free edge, directly above the tunnel.

The wall structure is another important distinguishing feature of *Plectogyra*. The wall is calcareous and contains a rather large amount of organic material. There is some evidence that the wall may be finely arenaceous, but it is altogether inconclusive. Some evidence also indicates that the wall of certain forms is composed in part of small, prismatic alveoli. This may account for the granular appearance of the wall of some specimens shown in accompanying photographs. Close examination at high magnifications under a petrographic microscope shows that the wall is composed of granules. Examination of the walls of fusulinids shows the same finely granular character. Under polarized light, the granules extinguish in different directions, indicating that there is no standard orientation of the crystallographic axes. The index of refraction of the granules is nearly identical to that of the surrounding crystalline calcite, so that no evidence is seen that the granules are composed of any substance other than calcium carbonate. An attempt to make an insoluble residue analysis of the shells of endothyroid foraminifers showed that the only material which remained after solution of the calcium carbonate with dilute hydrochloric acid was a small quantity of tectine. When the tectine was oxidized with concentrated nitric acid, examination of the residue showed no fragments of any kind which were visible under polarized light. Therefore, it may be assumed that if the shell of *Plectogyra* is arenaceous, the only particles which the foraminifer selected were composed of calcium carbonate.

One of the characters of *Plectogyra* is strongly indicative that the shell wall is not arenaceous. This is the ability of the foraminifer to secrete secondary deposits and subsequently to resorb these deposits partially. The secondary deposits are granular just like the rest of the wall. It seems doubtful that truly amorphous calcite can be deposited by any animal and it is unlikely that the endothyroid foraminifers were capable of transferring fragmental material through the protoplasm and depositing it within the shell. The transfer of calcite in chemical solution through protoplasm is accomplished by many animals. Since there is definite evidence of resorption of the secondary deposits, it must be assumed that the animal was capable of retaining calcium carbonate in solution in the protoplasm.

The cross-sectional appearance of the wall is nearly the same in *Endothyra* and *Plectogyra*. In both genera, there are two layers which are quite distinct and a third layer not present in all forms, which is less distinct. The secondary deposits of *Endothyra* and *Plectogyra* are remarkably similar in microscopic structure and they probably served the same purpose.

The size relationships of various shells which are considered to belong in *Plectogyra* are expected to aid in specific differentiation. The size differential is extremely large, some forms being six times larger than the smallest varieties. Size relationships of specimens of *Plectogyra* are more or less static within a single formation, even though the lithology may vary, and they show only restricted variation among formations belonging to a single series. However, between different series there may be exceedingly large differentials. These differences in size may be brought about by several factors influencing the environment. The amount of available food probably had the most pronounced effect. The environment of deposition does not seem to have had a pronounced influence upon size, since both the largest and smallest forms studied have been obtained from oölitic limestones.

COMPARISON OF FUSULINIDS AND ENDOTHYROIDS

The question of ancestry of the fusulinids has long been unanswered. A number of facts discovered by this study may throw light upon the problem.

The ways in which the endothyroids resemble the fusulinids may be enumerated as follows. The more primitive types of fusulinids and the endothyroids resemble each other strongly in the structure of the walls. The septa of both groups are produced by the downward curving of the outer spiral wall. Since the septa are extensions of the spiral wall which terminate at the septal edge, the spiral wall is itself discontinuous. Both groups possess a calcareous shell and both were capable of resorbing calcium carbonate after it had been deposited within the shell. Both precipitated secondary deposits and possessed a median tunnel, although the tunnel was produced in distinctly different ways by fusulinids and endothyroids. Certain species of fusulinids have so-called "endothyroid" juvenaria which seem to be coiled in nearly the same manner as *Plectogyra*. The majority of fusulinid species and all the members of the genus *Endothyra* are planispirally coiled throughout all stages of growth. The two groups seem to have chosen the same, or at least similar, environments in which to live, and in upper Chesteran and Lower Pennsylvanian rocks they are found together often. These are similarities which tend to link the fusulinids and the endothyroids, suggesting a phylogenetic relationship between them. On the other hand, there are enough differences between fusulinids and endothyroids to warrant their separation in two distinct groups and a listing of these dissimilar characteristics makes evident the conclusion that endothyroids do not belong in the family Fusulinidae.

The primitive fusulinids, which endothyroids most closely resemble, do not possess a true aperture at any growth stage. Both CUSHMAN and GALLOWAY consider the aperture of Foraminifera to be important in generic differentiation and the presence or absence of an aperture is judged to have sufficient importance to govern divisions between families. Since all endothyroids possess an aperture, this single important difference may be considered as significant enough to establish a definite separation between the endothyroids and primitive fusulinids. Considered as a whole, the shell walls of fusulinids and endothroids show certain very significant differences. It was originally thought that there were pore canals in the walls of the endothyroids, like those found in fusulinids. Observation of several hundred sections indicates that what were first thought to be pore canals are actually alignments of crystal grains in the wall. This phenomenon is not uncommon and has been observed in numerous sections, but every attempt to find true pore canals has been unsuccessful. It is believed that the crystal alignment may be caused by secondary crystallization or imperfect preservation of the original wall structure.

While endothyroids and fusulinids possess a median tunnel, the fusulinids develop the tunnel secondarily by resorption. DUNBAR & HENBEST (1942, p. 45) write as follows regarding the development of the tunnel in fusulinids:

> Until 1932 it was generally supposed that the tunnel was merely the trace of an external aperture. However, the shells with well-preserved antethecae never show such an aperture and if sagittal sections are cut it is found that the last several septa are complete at the middle of the shell. Since this is true at all stages of growth, it is evident that the tunnel is a secondary structure produced by resorption at the base of the septa some distance back of the antetheca.

The tunnel in the endothyroids is obviously the direct result of the aperture; however, there is some reason to believe that in many shells the original aperture is somewhat enlarged by resorption after the next chamber is added. The height of the aperture is normally a little less than the height of the tunnel. Both endothyroids and fusulinids are capable of resorption of calcium carbonate which was deposited as original shell material or as secondary deposits. The manner in which the resorption occurs and the area of the shell affected is different in the two groups. Resorption in the fusulinids occurs in the last chambers formed, whereas among endothyroids it takes place in the earlier part of the shell. The hooks or nodes in the endothyroids are commonly much more prominent in the last chamber and they are subsequently reduced in size or completely removed in the earlier chambers. Structural design of the septa of the fusulinids and endothyroids is markedly different. In the endothyroids, the chambers are swollen between the sutures and the septa curve away from the spiral wall in a nearly smooth arc, rather than nearly at right angles, as in the fusulinids. This tends to give the septa of the endothyroids a distinct anteriorly directed trend, an acute angle being formed between the front face of the septum and the spirotheca.

The fusulinids and the endothyroids possess secondary deposits, but they are entirely different in character and of different distribution within the shell. For example, the chomata of the primitive fusulinids never extend into the last chambers and they are absent commonly in the last half-volution, whereas the most prominent secondary deposits of endothyroids are found in the last chambers. The coiling of the endothyroids and fusulinids shows significant dissimilarities. The genus *Plectogyra*, which makes up a large percentage of the endothyroid group, differs greatly in its coiling from the normal planispiral type, which is characteristic of the fusulinids. Besides these features, none but the most primitive fusulinids have the axis of coiling shorter than the diameter of the shell.

STRATIGRAPHIC ZONES AND LOCALITIES STUDIED

This report covers a large area, most of which lies within the Mississippi Valley. Material has been obtained from outcrops in Missouri, Illinois, Iowa, Indiana, Tennessee, and Oklahoma. A large part of the Mississippian section has yielded endothyroids. Upper Devonian and Lower Pennsylvanian beds have been examined in order to understand better the phylogenetic trends shown by this group of foraminifers.

The Mississippian sequence of deposits in States of the Mississippi Valley just mentioned contains about 2,000 feet of primarily calcareous sediments. Most of the material used in the preparation of this report was taken from the type sections of the individual Mississippian formations. Material was provided from five of the formations discussed by geologists who were specially familiar with the section from which specimens were collected.

The use of type section material may have disadvantages inasmuch as the type exposures of the formations making up the standard Mississippian sequences are somewhat widely scattered geographically. Hence, lateral variation in fossil forms belonging to a given zone cannot be taken into account. This may lead to error in interpretation of phylogeny, but it should not lessen the stratigraphic value of the materials studied. In a few places, type sections were found to be incomplete, so that the rocks bounding them above and below could not be studied. Some of the type sections studied may not be actually representative of the general character of rocks of the same age. On the other hand, there are advantages in the use of type section material, for errors in correlation are eliminated and the type sections constitute standards of reference for problems in correlation.

DESCRIPTION OF LOCALITIES

UPPER DEVONIAN

Hackberry shale, Cerro Gordo member.—The sample from which all of the illustrated Devonian endothyroids in this paper were taken was collected in Cerro Gordo County, Iowa, in a quarry near Mason City. It consists of a light yellowish, slightly dolomitic clay shale which belongs to the Cerro Gordo member of the Hackberry shale (FENTON, 1919, p. 355). The sample yielded *Endothyra gallowayi* THOMAS in great abundance. Other samples of the Cerro Gordo were checked and all were found to contain these foraminifers.

KINDERHOOKIAN (LOWER MISSISSIPPIAN)

Hamburg oölite.—Samples were collected from the type section of the Hamburg oölite at Hamburg, Calhoun County, Illinois (WELLER, 1906, p. 464). The oölite grains of this formation, which belongs just above the Louisiana limestone, were found to have radial structure. No endothyroids were found.

Lower Chouteau and Chapin oölites.—An oölitic zone in the Mississippi River bluff at Burlington, Iowa, identified as belonging at the base of the Chouteau formation was sectioned and found to contain no endothyroids. Radial structure of the oölite grains like that of Hamburg oölite grains was observed. The Chapin oölite (VAN TUYL, 1925, p. 52), which occurs higher in the section at Burlington, was found to have concentric oölites, but they are so weathered that individual grains are clouded and almost all traces of fossils have been obliterated. The finding of minute chambered shells in some of the less altered grains indicates that examination of less altered rock may yield identifiable fossils.

Gilmore City limestone.—Oölitic beds of the Gilmore City limestone (VAN TUYL, 1925, p. 113) in Pocahontas County, Iowa, contain *Plectogyra* in great abundance. The upper part of this formation is predominantly oölitic, whereas lower strata are shaly and contain an abundant, well preserved crinoid fauna. This formation is identified as late Kinderhookian on the basis of both faunal and stratigraphic evidence (LAUDON, 1933). The endothyroid specimens illustrated in this report were obtained from a thin oölitic limestone occurring within the crinoidal zone. The lower part of the Gilmore City section contains lithographic limestone.

"Humboldt oölite."—Samples of the "Humboldt oölite" (VAN TUYL, 1925, p. 109) were obtained from the type section of this unit, presumed to belong near the top of the northern Iowa Kinderhookian sequence, at the town of Humboldt, Humboldt County, Iowa. *Plectogyra*, which was found high in the section, is a distinctly different species than the one occurring in the Gilmore City formation. Several beds of the "Humboldt" were found to contain endothyroids, those of the upper zone being best preserved.

OSAGIAN (LOWER MISSISSIPPIAN)

St. Joe formation.—The basal division of the Osagian rocks on the southwest flank of the Ozark uplift is the St. Joe limestone (MOORE, 1928, p. 160; CLINE, 1934, p. 1137). This formation was examined in outcrops at the west end of a highway bridge across an arm of Grand Lake about three miles west of the town of Wyandotte, on U. S. Highway 60, in Ottawa County, Oklahoma. The material obtained was taken from a conglomeratic oölite about 4 feet thick, which is exposed about 6 feet above lake level and directly below thin-bedded chert of the Reeds Spring formation. The rock consists of cobbles of strongly weathered white oölitic limestone 2 to 8 inches in diameter cemented by a finely oölitic groundmass. Thins sections of the limtstone cobbles show definite traces of *Plectogyra*, but no sections suitable for photographing were obtained. The groundmass is light gray in color and the oölites in it are much smaller than in the cobbles and they are unweathered. The endothyroids here observed are not contained in the oölite grains, as in other Mississippian formations so far described. The St. Joe endothyroid shells are free and in an excellent state of preservation. The fossil zone is directly below the St. Joe-Reeds Spring unconformity.

Keokuk limestone.—The upper Keokuk limestone (WELLER, *et al.*, 1948, chart), which belongs in the upper part of the Osagian succession, is well exposed in a quarry along the Mississippi River bank, about three miles south of the town of Montrose in Lee County, Iowa. Specimens were collected from the lower massive beds which have a dark bluish-gray color and numerous shale partings. Endothyroids contained in this material were free, no oölitic material being present. The upper portion of the quarry is more thinly bedded and is light yellowish brown in color, containing much crinoidal material and numerous shells of *Spirifer keokuk.*

Short Creek oölite.—A specimen of *Plectogyra* illustrated in this report was obtained from an outcrop of the Short Creek oölite, of Keokuk age, located 0.6 miles west of the town of Ritchie in Newton county, Missouri. The outcrop is in an old quarry north of Shoal Creek on the north side of the Frisco railroad tracks. About 6.5 feet of oölite is exposed here, most of it badly weathered (MOORE, 1925). The specimens of *Plectogyra,* which are exceedingly rare in this oölite, occur as free shells without an oölitic coating.

Warsaw formation.—Samples were collected from every limestone bed in the type section of the Warsaw formation in Soap Factory Hollow at the town of Warsaw, Hancock County, Illinois, (MOORE, 1928, p. 229; WILMARTH, 1938, p. 2276; WELLER, *et al.*, 1948, chart), and each one has been carefully sectioned and examined but no endothyroids have ever been obtained. The reason for such extensive examination of the section was on account of the proximity to the significant Osagian-Meramecian unconformity. Information is needed in this specific zone and further work should be done before the Warsaw is judged to be barren of endothyroids.

MERAMECIAN (UPPER MISSISSIPPIAN)

Endothyroid-bearing limestone in central Missouri.—On the west side of the Missouri River where Fish Creek crosses Highway "D" in Saline County, Missouri, a bed crops out which in lithology resembles closely that of upper strata in the section at Warsaw which have been included in the Warsaw formation. Numerous specimens of *Endothyra,* as well as *Melonechinus* and *Pentremites conoideus,* have been obtained from this bed. The presence of these fossils suggests that the zone belongs higher than rocks containing a different fauna which should be regarded as true Warsaw. It is possible that the Saline County limestone is transitional between Warsaw (Osagian) and Salem (Meramecian). This particular zone is the only one which has been found that contains symmetrical endothyroids in rocks which possibly may be classed as older than Meramecian.

Salem limestone.—Some specimens used in this report have been taken from the section of the Salem limestone (CUMINGS, 1901, p. 233) at Spergen Hill which is located several miles southeast of Salem, Washington County, Indiana. This formation, of undoubted Meramecian age, is called the Spergen limestone (ULRICH, 1904, p. 110; WILMARTH, 1938, p. 2039) by the U. S. Geological Survey and by some geologists. The largest specimens of *Plectogyra* so far observed have been obtained from a zone in the Salem in which the rock is made up almost entirely of the shells of endothyroid foraminifers.

A large number of endothyroids have been obtained from cable tool samples from a well located in the SE¼, SE¼, NE¼ sec. 19, T. 4 S., R. 7 W., Randolph County, Illinois. The specimens were collected in samples from a depth of 670-785 feet having what was called typical Salem lithology by the Subsurface Division of the Illinois State Geological Survey. Both *Endothyra* and *Plectogyra* are present in these cuttings.

A section which was measured at the crest of the Dupo anticline, about one-fourth of a mile east of the town of Dupo in St. Claire County, Illinois, begins in beds which resemble Salem in both lithology and fossil content. Limestones in the upper part of the succession studied here are definitely St. Louis in age. The rocks of Salem age yielded well-preserved specimens of *Plectogyra,* although they were not nearly so abundant as in samples of the Salem limestone from Indiana. The limestones of the Salem portion of the section from which the endothyroids were obtained are thin-bedded, finely fragmental, or slightly oölitic.

St. Louis limestone.—The upper part of the Dupo section corresponds to the St. Louis limestone (WILMARTH, 1938, p. 1880). It is highly variable in lithologic character and is probably cyclic in deposition. There are several zones of breccia and lithographic limestone beds alternating with shaly dolomitic beds. Specimens of dwarf *Endothyra* were obtained from a fragmental crinoidal limestone, but the lithographic units contain many specimens in an excellent state of preservation.

The St. Louis limestone was examined in a quarry in the southeastern portion of St. Louis, St. Louis County, Missouri, about six blocks from the Mississippi River bluffs. This quarry is now abandoned and partially filled in. The exposed beds are believed to belong in the upper part of the St. Louis formation. Endothyroids are scattered throughout the quarry section ,and they are unusually well preserved in some of the lithographic limestones. A thick brecciated zone at the bottom of the quarry is overlain by a slightly dolomitic, thick-bedded limestone. A prominent disconformity occurs at the top of this limestone, succeeding beds being shaly and containing some cross-bedded öolitic zones. Alternating beds of dolomite and lithographic limestone are well shown in the upper part of the section. Algal limestones and shales containing algal nodules are found near the top of the quarry. Corals and crinoids are present in some parts of the section and bryozoans are abundant. *Melonechinus* remains are very common near the bottom of the quarry.

Ste. Genevieve limestone.—Samples were collected from the upper Meramecian Ste. Genevieve limestone (Wilmarth, 1938, p. 1873) at its type locality, about one mile northwest of the town of Ste. Genevieve, Ste. Genevieve County, Missouri. The samples were taken from the south wall of the Ste. Genevieve Lime Company's quarry. Most of the section consists of massively-bedded oölitic limestone; a few beds are composed of fragmental crinoidal material. Some of the observed foraminifers in the oölitic zones are enclosed in the oölite grains, whereas others are free. Most of the specimens are very well preserved.

Chesteran (Upper Mississippian)

Paint Creek formation.—An outcrop of the Paint Creek formation in a creek bed one and four-tenths miles southwest of the town of Modoc in the western part of Randolph County, Illinois, was examined. This formation is the uppermost unit in the lower Chesteran New Design group and lies between the Bethel and Cypress sandstones (Weller, *et al.*, 1948, chart). The creek near Modoc flows south across the road and an abandoned road follows some distance upstream to a small waterfall at the base of which the red shales of the Paint Creek are exposed. The limestone ledges of the upper part of the formation form the waterfall and continue to outcrop some distance upstream. The limestones are finely fragmental, containing much crinoidal debris and many small bryozoans. In the upper part of the limestone section are several brown oölite beds in which the oölites show the beginning or radial crystallization but still possess well-defined concentric structure. A rather large number of minute gastropods are found in the oölites, but foraminifers are not common. The endothyroids are found free, none being enclosed in the oölite grains.

Glen Dean limestone.—The topmost unit of the middle Chesteran Homberg group is the Glen Dean limestone (Weller, *et al.*, 1948, chart). The outcrops of this formation were studied in a ravine south of Coles Mill in the town of Chester, Randolph County, Illinois, where most of the section is exposed. The lower part of the section is dark, massive crinoidal limestone and contains no endothyroids. The upper portion is finely oölitic and these beds yield common endothyroids. Several shale zones in the Glen Dean may yield endothyroids when washed.

Vienna formation.—In the upper Chesteran Elvira group, the Vienna formation is exposed in a roadcut of Illinois State Highway 150 about three-tenths of a mile east of the east end of the Chester highway bridge over the Mississippi River. This formation is separated from the Glen Dean limestone by the Tar Springs sandstone (Weller, *et al.*, 1948, chart). Samples were collected from the Vienna directly east of a concrete retaining wall along the road. A considerable thickness of shale occurs in the lower part of the formation but the upper part becomes more calcareous and the upper 16 feet are massive, thick-bedded gray limestone which is oölitic in some zones. From these oölitc beds both endothyroids and primitive fusulinids have been and primitive fusulinids have been collected. The endothyroids are represented by *Plectogyra* and the fusilinids by *Millerella.* Overlying the Vienna at this exposure is the cross-bedded, brown Waltersburg sandstone.

Clore limestone.—Upper Elvira beds belonging to the Clore limestone (Weller, *et al.*, 1948, chart) were sampled in a roadcut about 2.4 miles southeast of the town of Chester, Illinois. The limestone members of the Clore formation are best exposed in this cut on Illinois State Highway 3, about 500 feet northwest of the crest of the hill as the road ascends from the valley of the Marys River. The limestones are massive and the individual beds are separated by thin, gray shale partings which contain *Pentremites.* The rock contains scattered small oölites, but it is largely fragmental in character and very fine-grained. The endothyroids are generally free, but some are contained in oölite grains.

Kinkaid limestone.—The highest Chesteran formation, called the Kinkaid limestone (Weller, *et al.*, 1948, chart) is exposed in several gullies along the east side of Illinois State Highway 3, about 5 miles southeast of Chester. At this place, the basal sandstone of the Pennsylvanian rests directly upon the ledges of the Kinkaid. The Kinkaid is shaly in the lower part of the section and several thin shales separate the upper limestone beds. The limestones are finely fragmental, showing few oölites in any of the thin sections. The endothyroids are well preserved and invariably occur as free shells. *Plectogyra* is present in both the limestones and shales, and C. L. Cooper (1947, p. 81) has named several species of *Millerella* from this formation.

Atokan (Middle Pennsylvanian)

Ferdinand limestone in Indiana.—The Ferdinand limestone (Franklin, 1944) of early Atokan age exposed in the NW¼ sec. 20, T. 6 S., R. 4 W., Spencer County, Indiana, contains several shale zones and from one of these shales a specimen of a very advanced form of *Plectogyra* has been obtained. This particular specimen was taken from the shale directly below the limestone.

DESMOINESIAN (MIDDLE PENNSYLVANIAN)

Liverpool beds in Illinois. — The Liverpool cyclothem, of middle Desmoinesian age, contains a large microfauna. From the shale beds of the marine zone of the cyclothem three extremely advanced forms of *Plectogyra* have been obtained. The samples were collected in the SE¼ sec. 17, T. 8 N., R. 3 E., Fulton County, Illinois.

STRATIGRAPHIC DISTRIBUTION AND PHYLOGENETIC DEVELOPMENT OF ENDOTHYROIDS

By way of introduction to this section of the report, note is made that, excepting the form called *Plectogyra plectogyra*, n. gen., n. sp., no attempt has been made to define and describe new species of endothyroid foraminifers. Many new species have been encountered. Even a hasty examination of the plates of illustrations here published indicates differences between shells from various formations which are sufficient to warrant establishment of new species. Information concerning most of these forms is not yet adequate, it is believed, to permit description of them in a manner which will make them recognizable in sections cut in almost any plane. The preparation of standard sections having known orientation is one of the greatest difficulties, and this is an even greater problem when it is necessary to prepare thin sections from limestone fragments. Most of the sections illustrated in this report are rock sections which happened to encounter an endothyroid specimen. In all such sections, orientation of the specimen is at random.

Standard practice has been to saw the rock parallel to the bedding plane, inasmuch as most of the endothyroids, being discoidal, tend to lie with one of the flat surfaces parallel to the stratification. Sections cut in this manner are most likely to intersect the shell so as to show the coiling of chambers. The method works fairly well where the foraminifers are large enough to have a fairly flat surface, but it is not successful in limestones in which the shells are enclosed in oölite grains. In oölitic limestone containing foraminifers as the nuclei of oölites, no method has been found for orientation of the sections in advance of cutting the grains.

Another important factor affecting designation of new species is lack of information concerning the external appearance of the shells. A horizontal axial section commonly permits observations of the nature of the aperture and shows the amount of swelling of chambers between the sutures. Other sections are necessary to determine whether the shell is involute or evolute and in rocks sections it is not possible to be certain that the same forms are shown in two different sections. Accordingly, a large number of sections must be made before definition of new species can be undertaken. As a result, convenience in referring to groups of these shells by a species name has been sacrificed in order to avoid introducing inadequately defined species. A complete reclassification of all forms now refered to the genus *Endothyra* is needed, but the present study has stratigraphic value without undertaking this task.

DEVONIAN FORMS

THOMAS (1931, p. 40) has described foraminifers named *Endothyra gallowayi* from the Upper Devonian of Iowa. This form has planispiral coiling and is stated to resemble the genotype of Endothyra closely enough to warrant assignment to this genus. THOMAS considers the wall of *E. gallowayi* to be calcareous.

HENBEST (1935, p. 35) has described a Devonian coiled foraminifer which he designates as a new genus called *Nanicella.* Concerning the shell form and wall situation of *Nanicella,* Henbest states:

> Nanicella resembles *Orobias, Nummulostegina,* and *Staffella* somewhat more than *Endothyra.* In external form it resembles *Orobias* more closely, but differs significantly from that genus by being more discoid and less involute and having a chamber morphology that is less completely subordinated to the general plan of the shell. In comparison with *Endothyra, Nanicella* is considerably more advanced in regard to the degree of chamber subordination, although our present records indicate an earlier existence for *Nanicella. Endothyra,* as represented particularly by *E. bowmani,* the genotype, exhibits several so-called primitive traits not possessed by *Nanicella* in that it is irregularly coiled, its chambers are spherical in form, and a distinct boundary between the spiral and septal walls is absent.

Since publication of HENBEST'S paper, research on the type of shell coiling in the so-called asymmetrical group of endothyroids has been in progress. It is found that *Plectogyra* is coiled in a symmetrical geometric figure. The fact that the figure is a three-dimensional form which must be represented by two mathematical equations indicates that its symmetry is of a higher order than the two-dimensional planispiral form, which may be represented by a single equation. In both cases the initial form of the undistorted spiral is logarithmic. In the twisted form, the distortion is caused by the rotation of the plane in which the spiral is generated. The plane is rotated about an axis which has the origin of the spiral as its midpoint. Another equation must, therefore, be combined with the equation of the logarithmic spiral to represent the rotation of the plane of generation. If the symmetry of the plectogyroid forms is of a higher order than the symmetry of the planispiral forms, one might expect to find that the planispiral forms begin at a lower stratigraphic level than the plectogyroid types.

THOMAS (1931, p. 40) states in his description of *Endothyra gallowayi:*

> . . . in some specimens the wall has a thin, dark outer layer and a thicker inner layer corresponding to the tectum and keriotheca of *Triticites.* . . .

It seems more logical to compare the wall of *E. gallowayi* to the wall of one of the primitive fusulinids, rather than that of the somewhat advanced shell of *Triticites*. The fact remains, however, that there are two distinct layers in the wall which makes the similarity between this form and the rest of the endothyroid group very definite. Taking account also of the planispiral coiling of this species, the name *Endothyra gallowayi* is judged to be valid. This form may be ancestral to *Plectogyra,* oldest known representatives of which occur in upper Kinderhookian (Lower Mississippian) rocks. By what process the planispiral form in the Devonian could give rise to the three-dimensional forms of the Kinderhookian is not known. No lower Kinderhookian or post-Hackberry Devonian endothyroid forms, which might show characters intermediate between typical *Endothyra* and *Plectogyra,* have been available for study. When some such forms are discovered, the relationships may be more fully understood.

Two distinctly different types of shell design are seen in the specimens from the Cerro Gordo beds. Both are planispirally coiled, but one shell expands more rapidly than the other. Plate I, figure 10, shows the rapidly expanding spiral form. This specimen has two and three-fourths volutions. It is larger and the chamber height in the last volution is greater than in the more tightly coiled form. The tunnel is well shown, but the antetheca is broken away so that the aperture is not visible. The wall structure is not clearly shown in any of the specimens and commonly the preservation is very poor, but the tectum is plainly visible in some portions of the shell in figure 10. Plate I, figure 14, shows a juvenile form of the rapidly expanding variety.

The more tightly coiled forms are shown in Plate I, figures 12, 13, and 15. This is most common in the samples from which the specimens were obtained. The closely coiled specimens are smaller in diameter, but they possess as many volutions as do the rapidly expanding shells. All of the specimens shown are probably adult forms.

The phylogenetic relationship of this group of endothyroids to observed forms above and below the Cerro Gordo is very uncertain. They may have been derived from unchambered Foraminifera such as *Ammodiscus* or *Glomospira*. *Glomospira* seemingly coils in a plectogyroid spiral; therefore, it is possible that *Glomospira* gave rise to *Plectogyra* and *Ammodiscus* may have given rise to *Endothyra*. If this is true, the relationship of *Endothyra* to *Plectogyra* represents a nearly perfect example of parallel evolution.

If *Endothyra,* as represented by the Cerro Gordo specimens, is actually derived from *Ammodiscus,* it is logical to assume that the more closely coiled form is the more primitive of the two varieties, since *Ammodiscus* expands very slowly. Further research will be necessary and transitional forms must be found before *Endothyra* and *Ammodiscus* can be linked as members of an evolutionary sequence.

KINDERHOOKIAN FORMS

The endothyroids found in Kinderhookian strata are distinct from those of Devonian age both in coiling and structural design of the shell. The first, and probably the most important, single factor which distinguishes the Kinderhookian from the Devonian endothyroid faunas is the total absence of Kinderhookian planispiral forms. All known endothyroids from this part of the Lower Mississippian deposits belong to the genus *Plectogyra*.

The same difficulties are encountered in making measurements of the shell dimensions of the Kinderhookian members of *Plectogyra* as are found in dealing with the younger forms. The Kinderhookian shells are within the central portion of the size differential range and the chambers are fewer in number than in the more advanced types. Since the chambers are fewer in number, they are larger in proportion to the size of the shell than in any of the younger forms. The chambers are strongly swollen between the sutures.

The attitude of the septa is distinctly acute and directed forward in most specimens. The septa are short and the chambers are normally low. The wall structure is indistinct in most of the studied specimens because preservation is poor. It is composed of two layers. Secondary deposits are nearly or entirely lacking. No hook-shaped deposits have been found in any Kinderhookian or Devonian endothyroids.

The coiling of the Kinderhookian form is of particular significance, since *Plectogyra* first appears at this time. As mentioned before, the genus *Glomospira,* which is first found in the Silurian, coils in a plectogyroid spiral, and this gives considerable weight to the possibility that *Plectogyra* may be evolved from *Glomospira* rather than from a planispiral ancestor. The angles of rotation between the half volution planes are probably not large and may be fairly small. Since no controlled sections could be obtained, it has not been possible to measure the angles of rotation in any of the specimens illustrated in this report.

All of the specimens available for study were enclosed in oölite grains. Attempts were made to obtain free specimens by crushing the limestone, but even when the individual oölites were freed, some which contained endothyroids could not be distinguished from those which did not. Greater difficulties were encountered in studying the Kinderhookian rocks and endothyroid faunas than in work on any other part of the geologic section. All of the foraminiferal shells in these rocks were found to be encased in a thick outer coating of oölitic material which made it difficult to distinguish between the outer boundary of the shell and the oölitic precipitate. This condition contributes to a misleading impression of unusually thick walls. Specimens which show the true thickness of the wall reveal its actual somewhat greater thickness in proportion to the size of the shell than is seen in any younger forms. Further studies of Kinderhookian rocks may lead to finding some free specimens so that oriented sections may be prepared. The fact that all of the sections illustrated from the Kinderhookian are rock sections and therefore unoriented has caused serious difficulties. It has been nearly impossible to obtain enough sections which were near standard orientation to make adequate comparison with other forms. Because the specimens in both the Gilmore City limestone and the Humboldt oölite form the nuclei of oölites, none of the usual methods of obtaining even partially oriented sections can be used. After the shells have become coated with a layer of calcite, they are nearly spherical and there is no longer any tendency to come to rest with the flat sides of the shell parallel to the bottom. Furthermore, many of the oölitic limestones from which these specimens have been taken are cross-bedded, so that even if some trace of the flat surface does remain, it has little effect on the position in which the grain comes to rest.

It seems clear that none of the foraminifers found in the Gilmore City and Humboldt oölites were alive at the time of their burial in the sediments, providing the oölites were developed before deposition. No free, uncoated shells have been found. Enough time must have elapsed after the animal died and before final deposition to allow the coating of calcite to collect on the surface of the shell. The foraminifers may have lived in an environment different from the one in which the oölites were developed. If the oölite grains formed along shorelines, as many authors believe, much lateral transportation may have taken place between the place of origin of the shells and the final location of deposition. Definite conclusions may not be drawn when the only material available for study is preserved in this manner.

The endothyroids which have been sectioned from the Gilmore City are illustrated on Plate 1, figures 1-9 and 11, and Plate 2, figures 19 and 20. The most nearly oriented horizontal axial sections are shown in Plate 1, figures 5, 6, and 8. Plate 1, figure 1, shows the flattened character of the chambers and the acute, strongly forward-directed attitude of the septa. Plate 1, figure 5, shows extreme shortening of the septa, probably by resorption. This specimen also shows the angles of rotation of the various coiling planes of the inner volutions and is well centered, so that the proloculus can be seen. Plate 1, figure 7, is a section of an unusual form, which differs from average shells in structural design and in rate of expansion of the coil. The section is off-center, but the septa and the shape of the chambers are well shown. It should be noted that the septa are longer, the chambers more compressed, and the attitude of the septa different from these characters in any of the other specimens. The rate of expansion of the coil is similar to that of the rapidly expanding form in the Cerro Gordo beds. Plate 2, figures 19 and 20, present slightly oblique vertical axial sections which illustrate the coiling and extreme shortening of the septa of the inner volutions.

The sections from the Humboldt oölite are shown on Plate 2, figures 15, 18, 21, and 22. The forms from the Humboldt are somewhat more compressed laterally and the walls are mostly thinner than those of Gilmore City specimens. They are also generally a little smaller, although the specimen shown in figure 22 is nearly as large as the largest endothyroid found in the Gilmore City. Plate 2, figures 15 and 22, are vertical axial sections showing the normal chamber arrangement in this type of section. A fairly well centered horizontal axial section, illustrated in Plate 2, figure 18, shows the aperture and the small number of chambers in the last volution. The specimen shown in Plate 2, figure 21, is an almost perfectly oriented transverse section, cut at right angles to the axis of crossing of the half-volution planes. This section is so well oriented that the angles of rotation can be measured. These angles are found to be fairly small, being nearly the same as those of the Gilmore City forms.

The phylogeny of the Kinderhookian endothyroids is not well known because of the scarcity of fossils of this group below the upper zones. Two possible ancestral stocks may have given rise to *Plectogyra*. CUSHMAN (1940, p. 97) states that chambered forms develop from unchambered, tubular forms. If this is true, the ancestor of *Plectogyra* is probably *Glomospira,* which occurs in Upper Silurian deposits and is coiled in a plectogyroid spiral. If the chambered form were evolved before the end of Devonian time, one might expect to find *Plectogyra* in the Cerro Gordo beds of Iowa. Since the genus is not known in Devonian rocks, one may judge that *Plectogyra* did not develop until Mississippian time.

Possible ancestry of the Kinderhookian endothyroids which should not be ignored is represented by unchambered foraminifers having a distorted spiral form of coiling like *Plectogyra.* No change would be involved in the form of the equation representing either the chambered or the unchambered form, so that this development would be of minor consequence if the process of evolution follows mathematical laws. The development of a plectogyroid spiral from a plane spiral, on the other hand, requires the introduction of another equation to represent the rotation of the plane.

So far, most of the evidence presented favors the conclusion that *Plectogyra* developed from *Glomospira.* There are important factors, however, which offer evidence for development of *Plectogyra* from

Endothyra. No forms resembling *Plectogyra* have been found in Devonian rocks. Chambered forms, such as the one already described, were abundantly present at the end of the Devonian. If one assumes that *Endothyra* and *Plectogryra* represent two members of a sequence of parallel evolutionary forms, the development of *Plectogyra* from *Endothyra* seems logical. The development of secondary deposits, which are exactly alike and which appear at the same stratigraphic level in both genera, and the similar attitude of the septa at the same stratigraphic position are evidence of parallelism. The fact that both coil in a logarithmic spiral is also significant. There is great variation in the degree of rotation of the coiling planes and some forms show such slight variation that the total angular rotation of all the planes of the entire shell approaches zero degrees. If the angle is so slight as not to be noticed in the section, the form would be classified incorrectly as *Endothyra,* instead of *Plectogyra.*

OSAGIAN FORMS

Comparison of the Osagian endothyroids with those of Kinderhookian age indicates close phylogenetic and structural relationalship but definite advancement of Osagian specimens in general shell form. The major, immediately apparent, difference is the variation in size. This is especially true in the lowermost Osagian forms, which are commonly one-half to one-third the size of the Kinderhookian specimens. The preservation of most Osagian forms is superior to that of the Kinderhookian shells, wall structure being unusually well shown.

The final volution of Osagian endothyroids commonly contains six or more chambers which are less swollen between the septa than in Kinderhookian forms. All observed Osagian shells have much thinner walls, also, than earlier Mississippian endothyroids, but this feature may be due at least partly to smaller size of the shell and consequent thinning of the wall in proportion to the reduction in size. When the average thickness of the wall is considered in comparison with the diameter of the shell, however, the relative wall thickness of the Osagian forms is found to be about one-half the relative thickness of the Kinderhookian forms. The attitude of the septa is less acute except in upper Osagian forms which have distorted final chambers. Commonly, only three volutions occur in the adult form and the total angle of rotation is somewhat larger than that of the Kinderhookian forms.

Variation in form is observed among the Osagian endothyroids which is not surprising in view of the fact that the only Osagian forms available for study have come either from the base or the top of the Osagian section. No intermediate forms have been seen. The St. Joe endothyroids resemble the Kinderhookian types in several respects, whereas the Keokuk specimens show much less similarity to the Kinderhookian. Also, the St. Joe shells show no evidence of secondary deposits at any stage of development, while Keokuk forms possess very rudimentary nodes or mounds on the floor of the chambers behind the septa. The average size of the Keokuk specimens is slightly larger than those from the St. Joe, but, taken as a whole, all of the Osagian forms fall at the lowest end of the size differential. In fact, the smallest endothyroids found in any part of the section come from the St. Joe formation.

The collapse of the final two or three chambers of the endothyroid shells seems to be peculiar to upper Osagian specimens. This feature was first seen in the section of an endothyroid from the Short Creek oölite of southwestern Missouri. It may have been injured or crushed and the growth arrested in the final chambers. Two specimens were found in the Keokuk limestone in southeastern Iowa which also showed this same character. Only one specimen has been found in upper Osagian beds

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EXPLANATION OF PLATE 1

All figures × 100

FIGURE		PAGE
1, 2, 5, 9	—*Plectogyra sp.* Horizontal axial sections showing arrangement of internal volutions; Gilmore City formation, Lower Mississippian (Kinderhookian), Gilmore City, Iowa.	11
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7	—*Plectogyra sp.* Horizontal axial section of an unusual form showing rapid rate of expansion of the shell coil; Gilmore City formation, Lower Mississippian (Kinderhookian), Gilmore City, Iowa.	11
10	—*Endothyra gallowayi* (HENBEST). Cross section of the rapidly expanding form showing the marked increase in the height of the chambers of the last volution; Cerro Gordo formation, Upper Devonian, Mason City, Iowa	10
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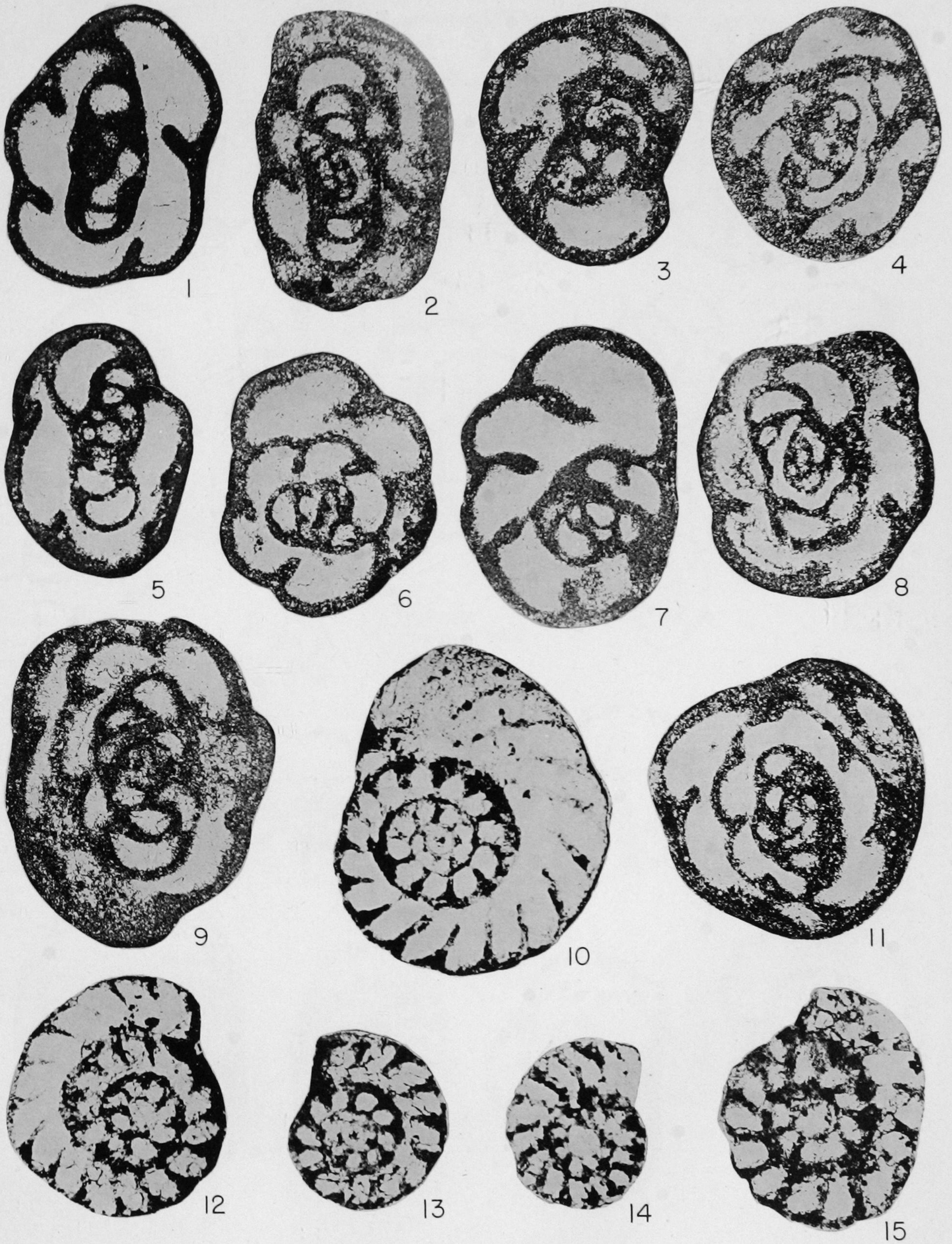
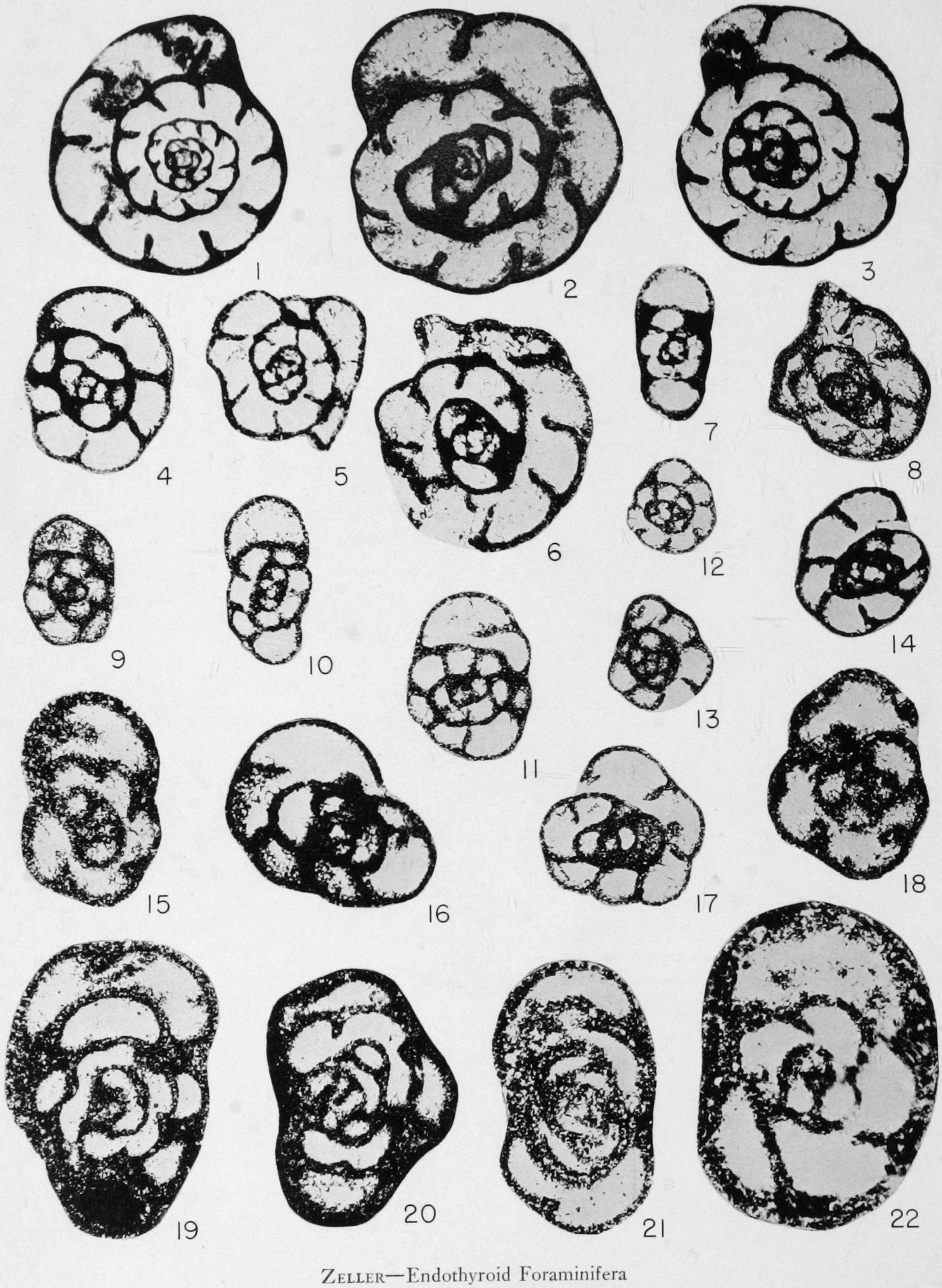
12, 13, 15	—*Endothyra gallowayi* (HENBEST). Cross sections of tightly coiled forms, all adults; Cerro Gordo formation, Upper Devonian, Mason City, Iowa	10



ZELLER—Endothyroid Foraminifera



Zeller—Endothyroid Foraminifera

which does not show distorted final chambers. The specimens having collapsed final chambers—one from the Short Creek oölite and others from the Keokuk—were collected at localities about 300 miles apart, which possibly represent different basins of deposition. The characteristics of distorted final chambers is fairly widespread. The collapse of the last chambers is not judged to constitute a mutational development.

Explanation for the unusually small size of the Osagian endothyroids is not known. The fragmental nature of many of the Osagian limestones suggests that the environment in which they were deposited may have been unfavorable for these foraminifers, leading to reduced numbers as well as marked diminution in size. Endothyroids are nowhere common in highly crinoidal limestones and are not normally associated with molluscan faunas. A scarcity of food may have been a factor. Whatever the cause of reduced numbers and small size of the Osagian endothyroids, these vanished completely by the beginning of Meramecian time, since it is in the rocks of the lower part of this division of the Mississippian sequence that the largest endothyroids are found.

None of the Osagian forms are encased in oölitic material. The shells are conmmonly free, indicating that the animal lived in the environment in which the shells were deposited. It seems quite unlikely that the fragile, thin-shelled forms found in the Osagian rocks would be preserved if they had been transported very far. Already mentioned, however, is occurrence of endothyroids in a conglomerate of the St. Joe formation directly below the unconformity at its top. This conglomerate and the associated oölitic groundmass must have been deposited near a shore which was subjected to enough wave action to account for the presence of large cobbles in the conglomerate, derived probably from rocks above sea level.

The most typical appearance of St. Joe endothyroids, as seen in horizontal axial sections, is shown in Plate 2, figures 12, 14, and 17. Well-oriented vertical axial sections (Pl. 2, figs. 10, 11) show the coiling planes of the internal volutions. The height of the aperture is indicated in Plate 2, figures 14 and 17. The smallest endothyroid found, believed to be an adult form, is illustrated in Plate 2, figure 12. The wall structure is not well indicated by the photographs, because the walls of the St. Joe forms are extremely thin.

The single specimen from the Short Creek oölite is illustrated in Plate 2, figure 8. The collapsed condition of the final chambers is well shown. Plate 2, figure 4, represents the only specimen found in upper Osagian rocks which does not show distortion in the last chambers. This specimen is from the Keokuk limestone. The figure shows a nearly perfectly oriented horizontal axial section through the proloculus. The attitude of the septa and the presence of a rudimentary type of secondary deposit in the penultimate chamber can be seen. The largest specimen found in Osagian rocks is illustrated in Plate 2, figure 6. The wall structure of this

EXPLANATION OF PLATE 2

All figures × 100 except as recorded otherwise.

FIGURE		PAGE
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18	*Plectogyra sp.* Horizontal axial section showing aperture; Humboldt oölite, Lower Mississippian (Kinderhookian), Humboldt, Iowa	11
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specimen is fairly well shown. Secondary deposits and the distorted shape of the final chamber are evident. The form shown in Plate 2, figure 5, shows the maximum amount of distortion found in any endothyroid thus far studied. The last three chambers of this specimen are altered.

The phylogenetic relationships of Osagian endothyroids seem to be fairly clear. Other than distortion of the final chambers of some upper Osagian shells, nothing unusual appears in the group. A normal evolutionary sequence between Kinderhookian and Meramecian forms is indicated. The development of higher angles of rotation between the half-volution planes and the appearance of secondary deposits in the Keokuk forms provides a transitional sequence which fits perfectly between the simpler, more primitive forms occurring below and the more advanced forms occurring above.

No planispiral endothyroids have been found in rocks of Kinderhookian or Osagian age. The question of seeming absence of *Endothyra* in the lower half of the Mississippian cannot be answered on the basis of information now at hand. Two possible explanations can be offered but neither is satisfactory. According to one hypothesis, planispiral endothyroids may be entirely lacking between Upper Devonian and lower Meramecian horizons. If this is true, we must assume that *Endothyra* developed from *Plectogyra* in late Osagian or early Meramacian time. Another hypothesis postulates that the genus *Endothyra* actually is present in both Kinderhookian and Osagian rocks but it has not been found. This would explain the presence of an advanced type of *Endothyra* in Meramecian strata by assuming normal evolution through forms thus far unknown. The fact remains that rocks of several Kinderhookian and Osagian formations have been sectioned extensively without finding any planispiral endothyroids.

OSAGIAN-MERAMECIAN BOUNDARY

The changes in form of the entire endothyroid group which occur immediately above the Osagian-Meramecian unconformity are so marked as to indicate that this break is the most prominent in the entire Mississippian section. Insofar as endothyroids are concerned, it is even more striking than the break between Mississippian and Pennsylvanian. Most important is the appearance of *Endothyra* and *Plectogyra* in rocks of the same age.

In Devonian rocks only the planispiral forms are seen, no plectogyroid types having been found. In Kinderhookian and Osagian formations, the reverse is true, plectogyroids being present but no planispiral forms. At the base of the Meramecian section, however, both genera are present in abundance. Below the Osagian-Meramecian unconformity, evolution of *Plectogyra* seems to have proceeded at a slow rate, no especially marked changes being noted among shells which form a transitional series. Above this boundary the number of endothyroids present in the rocks is greatly increased and the size of the forms attains maximum development in the basal Meramecian deposits.

The presence of *Endothyra* in rocks which lithologically and paleontologically resemble the Warsaw formation at its type section introduces several problems. Such rocks are exposed near Lisbon, in north central Missouri, about 150 miles from the type section of the Warsaw. Rocks of the Warsaw type section have been sampled rather thoroughly and thin sections of them have been prepared. The limestones are found to be fragmental, containing much crinoidal material and commonly containing 30 to 50 percent glauconite. No endothyroids have been found in the rocks of the Warsaw type section. At Lisbon, the limestones are finely fragmental and glauconite is present only in small

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EXPLANATION OF PLATE 3

All figures × 100 except as recorded otherwise.

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2—*Plectogyra plectogyra* n. gen., n. sp. Horizontal axial section of the holotype; St. Louis formation, Upper Mississippian (Meramecian), St. Louis, Missouri......	3, 17
3—*Endothyra sp.* Cross section of well preserved specimen showing shortened septa; St. Louis formation, Upper Mississippian (Meramecian), St. Louis, Missouri.......	17
4, 6—*Endothyra sp.* Cross section of dwarf forms; St. Louis formation, Upper Mississippian (Meramecian), St. Louis, Missouri........	17
5—*Endothyra bowmani* BROWN, Photographic reproduction of the holotype copied from *Elements of Fossil Conchology*, Sir THOMAS BROWN, 1843, figure 2, plate VI. The figure appears here almost two times its original size. Assumed magnification of the holotype (× 100).....................	3
7, 11, 13—*Endothyra sp.* Cross sections of rapidly expanding forms showing hooks; well cuttings from the Salem formation, Upper Mississippian (Meramecian), Randolph County, Illinois (× 50)..........................	16
8, 9—*Endothyra sp.* Cross sections of tightly coiled forms; well cuttings from upper part of Salem formation, Upper Mississippian (Meramecian), Randolph County, Illinois. (× 50).	16
10—*Plectogyra sp.?* Horizontal axial section of a form with extremely small angles of rotation; well cuttings from Salem formation, Upper Mississippian (Meramecian), Randolph County, Illinois (× 50)...........	16
12—*Plectogyra sp.* Horizontal axial section of largest specimen found; Salem formation, Upper Mississippian (Meramecian), Spergen Hill, Indiana (× 50)................	16
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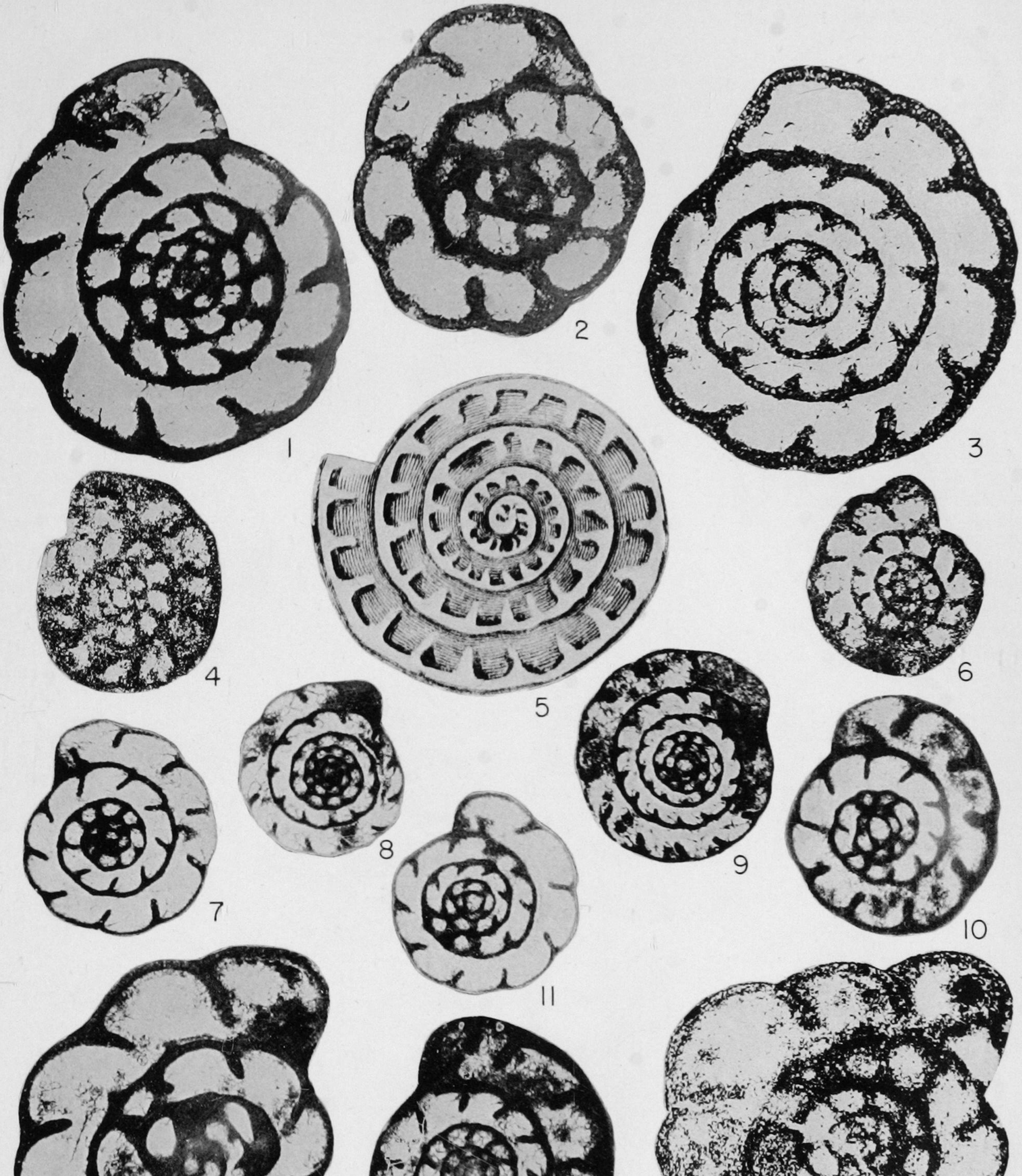
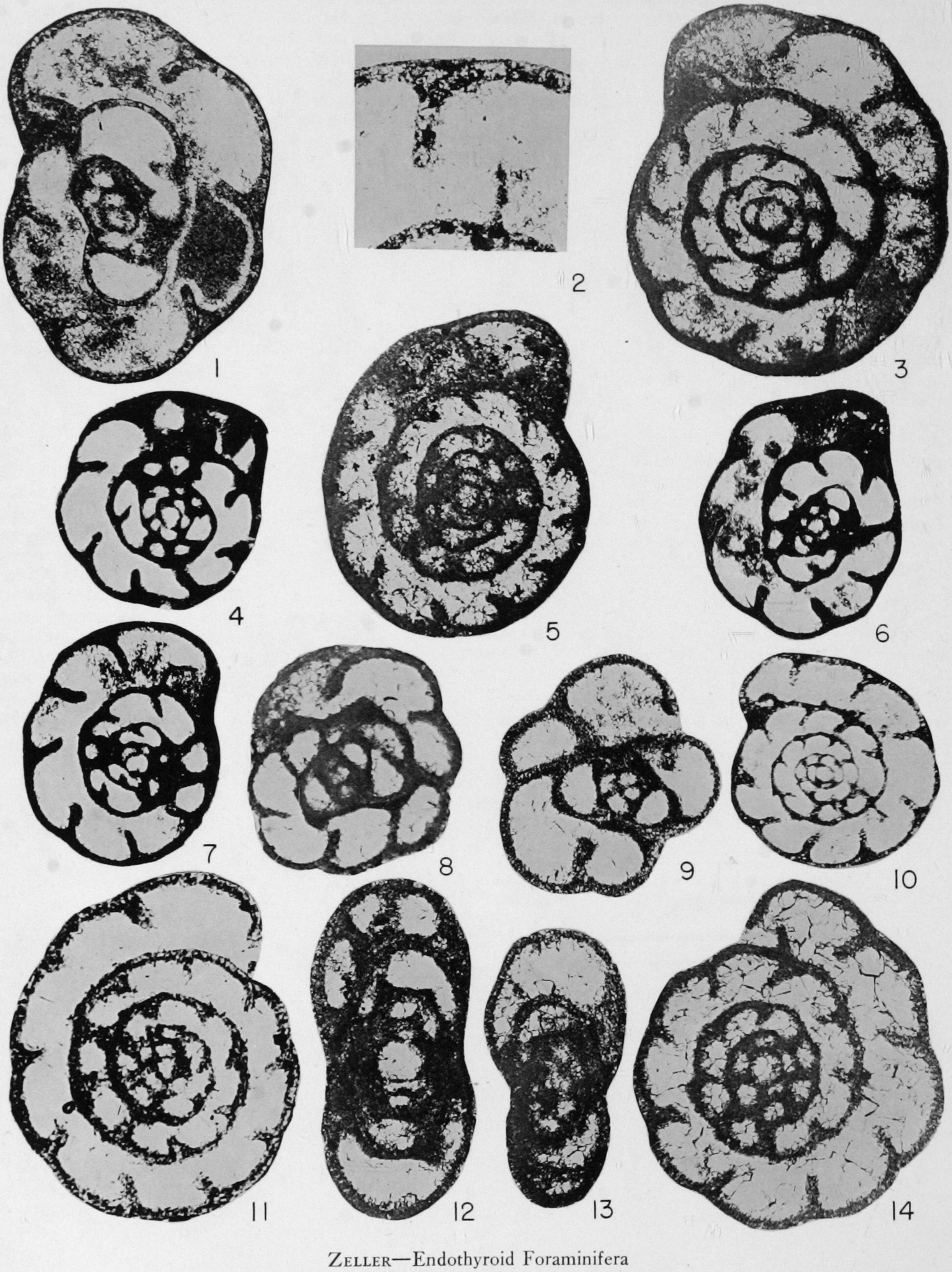


Zeller—Endothyroid Foraminifera



Zeller—Endothyroid Foraminifera

amounts. Stratigraphic correlation of these beds with type Warsaw or with higher strata of Meramecian age is uncertain. The Lisbon rocks may correspond to the Salem formation, representing near-shore deposition of early Meramecian age. Endothyroids collected from these rocks show strong Salem affinities. A typical specimen of *Endothyra* from limestone at Lisbon is shown in Plate 3, figure 1.

MERAMECIAN FORMS

The limestones of Meramecian age in the central Mississippi Valley region have been more extensively studied in the preparation of this report than any other Mississippian rocks because endothyroids are most aboundant in these strata. About 60 percent of the rocks in the Meramecian section of the Mississippi Valley, when studied in thin section, yield endothyroids. In some restricted zones the shells of endothyroid foraminifers are so abundant that they make up nearly 80 percent of the rock. As is often true in the lower part of the Mississippian section, the endothyroids of Meramecian rocks are commonly associated with oölitic limestones. There are exceptions, however, especially in the St. Louis formation, in which the endothyroids commonly occur in lithographic or, less commonly, in crinoidal limestones.

Salem Endothyroids

So much more information has been obtained about endothyroids of the Meramecian formations that it is desirbale to consider them separately.

The endothyroid fauna of the Salem limestone has a distinctly different aspect than that of any lower zone. Both *Endothyra* and *Plectogyra* occur together in the same beds and the ratio of one to the other seems to have stratigraphic significance, although this may be limited to local areas. The Salem endothyroids attain the largest size of any observed in the Mississippian section, the diameter of one of the largest forms being about 1.8 mm. The variation in size between Osagian and Meramecian forms is particularly marked and this distinction seems to hold throughout a wide area.

The genus *Plectogyra* seems to be represented by only one species in the Salem—at least all endothyroids from Salem beds available for this study are very closely related. The observed Salem specimens are about six times the diameter of the smallest adult form in the St. Joe formation. The shells belonging to *Plectogyra* have angles of rotation which are intermediate between the known lower and higher variations of these angles. The walls are thick and the septa are curved strongly forward. Secondary deposits occur far back in the shell but evidence of partial resorption is found in the nature of the deposit in the final chamber. This invariably is developed as a sharply pointed hook-shaped projection, whereas all other deposits appear as low rounded mounds. The hook is actually the cross-sectional view of a continuous or discontinuous ridge from which a curved shelf projects forward from the top. This ridge and shelf may have served as a vestibule behind the aperture. A very unusual type of secondary deposit in some Salem plectogyroids takes the form of a thickening of the free edge of the septum directly above the tunnel, most of the material being added to the posterior side of the septum. The secondary deposits, especially the thickening of the septal edges, are

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EXPLANATION OF PLATE 4

All figures $\times$ 100 except as recorded otherwise.

Figure		Page
1	*Plectogyra sp.* Horizontal axial section of elongate form showing very thin walls and hook-shaped deposit in last chamber; Ste. Genevieve formation, Upper Mississippian (Meramecian), Ste. Genevieve, Missouri...	17
2	*Endothyra sp.* Wall structure of form shown in figure 10 of this plate ($\times$ 250).........	18
3, 5	*Endothyra sp.* Cross sections showing secondary deposits; Ste. Genevieve formation, Upper Mississippian (Meramecian), Ste. Genevieve, Missouri................	18
4	*Plectogyra sp.* Horizontal axial section of discoidal form; Ste. Genevieve formation, Upper Mississippian (Meramecian), Ste. Genevieve, Missouri ($\times$ 50)............	18
6, 7	*Plectogyra sp.* Horizontal axial sections of common elongate forms; figure 7 shows well developed hook in final chambers; Ste. Genevieve formation, Upper Mississippian (Meramecian), Ste. Genevieve, Missouri ($\times$ 50)........................	17
8	*Plectogyra sp.* Horizontal axial section showing secondary deposits; St. Louis formation, Upper Mississippian (Meramecian), St. Louis, Missouri.......................	17
9	*Plectogyra sp.* Oblique section showing the aperture; St. Louis formation, Upper Mississippian (Meramecian), St. Louis, Missouri.	17
10	*Endothyra sp.* Cross section showing well developed hook in final chamber; Ste. Genevieve formation, Upper Mississippian (Meramecian), Ste. Genevieve, Missouri ($\times$ 50).	18
11, 14	*Endothyra sp.* Cross sections showing apertures, hook is well shown in figure 14; St. Louis formation, Upper Mississippian (Meramecian), St. Louis, Missouri........	17
12, 13	*Endothyra sp.* Axial sections, slightly oblique; St. Louis formation, Upper Mississippian (Meramecian), St. Louis, Missouri.	17

shows most of the characteristics of the St. Louis forms. Plate 4, figure 8, which is a photograph of another specimen from the same section shows very large mounds in the last two chambers. These mounds are fused together at the base. An inclined section of *Plectogyra* showing the aperture is illustrated in Plate 4, figure 9.

Undoubtedly, the St. Louis forms of *Plectogyra* are descended from Salem antecedents which they resemble in all but minor details of the character and location of secondary deposits. The St. Louis forms follow the general trend among endothyroids toward increase in size and augmentation of secondary deposits.

Specimens of *Endothyra* are somewhat more common in the St. Louis limestone than those belonging to *Plectogyra*. Two distinct types of *Endothyra* occur, one of which is a dwarf and the other normal in size. The spiral coiling of the two shells differs less than in the tightly coiled and rapidly expanding Salem forms. The St. Louis endothyroids lack prominent secondary deposits and there is evidence of shell resorption. The walls of most specimens are slightly thinner and the septa are generally shorter than among Salem specimens. Three and four volutions occur in adult shells.

The dwarf endothyroids found in the St. Louis limestone represent an unusual development, for similar shells have not been encountered in any other material studied; also, both *Endothyra* and *Plectogyra* of normal size occur in beds above and below the zone containing the dwarfs. The diminutive size of the dwarf forms, which occur in a coarsely fragmental crinoidal limestone, probably indicates unfavorable environmental conditions. This rock contains no normal-sized forms, such as those found in lithographic and oölitic limestones. The dwarf specimens resemble normal ones in all respects except size. Typical examples are illustrated in Plate 3, figures 4 and 6. Adult specimens of the normal variety are shown in Plate 3, figure 3, and Plate 4, figures 11 and 14. The hook is especially well shown in Figure 14. Typical cross sections of *Endothyra* from the St. Louis limestone are seen in Plate 4, figures 12 and 13. These sections seem to be slightly asymmetrical but this may be partially due to the inexact or slightly inclined orientation of the sections. Secondary deposits shown in Plate 4, figure 12, somewhat resemble the chomata of primitive fusulinids. The preservation of the specimens is such that the walls and secondary deposits are indistinct and it is impossible to be certain that they have not been altered slightly.

Interpretation of the phylogeny of St. Louis representatives of *Endothyra* is somewhat complicated by the nature of the spiral. It is uncertain whether the St. Louis form is derived from the rapidly expanding form of the Salem or the more tightly coiled form, for the spiral expands at an intermediate rate. The secondary deposits of the St. Louis shells are more restricted and in this respect they seem to resemble the more tightly coiled Salem endothyroids.

STE. GENEVIEVE ENDOTHYROIDS

The St. Genevieve limestone yields endothyroids which in most respects resemble those of the St. Louis. The conditions of sedimentation represented by limestones of the type section of the Ste. Genevieve are evidently very similar to those of the Salem. Most of the specimens were taken from oölitic beds but some were obtained from a bed of crinoidal limestone near the base of the section. The Ste. Genevieve strata contain abundant endothyroids throughout the section, although they are no where as plentiful as in the Salem. Some of the Ste. Genevieve oölitic limestones contain endothyroids which form nuclei of the oölites, whereas other oölitic beds contain free shells, which are not coated with calcite.

Specimens of *Plectogyra* found in the Ste. Genevieve limestone are more variable than in any of the lower formations. All show general similarity in coiling and degree of rotational distortion, but considerable differences appear in the shape of the shells. Most Ste. Genevieve plectogyroids show a definite tendency toward elongation of the shell, especially in the upper part of the section. The significance of this elongation is not clear but it may be caused by rotational distortion of the spiral which is somewhat greater than among specimens from the lower part of the Meramecian section. The chambers generally are strongly swollen between the sutures. The size and shape of the chambers varies according to the position in the shell, especially in the elongated forms. The septa are commonly long and anteriorly-directed but their attitude is also controlled by their position in the shell. Secondary deposits are present in all of the specimens and are of two types. The septa of some shells show thickening on the posterior side of the free margin. Hooks are well developed in the last chamber, but they are almost completely removed by resorption in all of the preceding chambers. Commonly, the hooks are at least half the height of the chamber, but they are thinner and less massive than those in Salem and St. Louis forms. The inner wall is exceptionally thin, probably as result of the removal of all of the secondary material by resorption.

A typical horizontal axial section of a Ste. Genevieve endothyroid which shows a well-developed hook and extremely thin inner wall is illustrated in Plate 4, figure 1. Typical elongated forms (Pl. 4, figs. 6, 7) show variation in the attitude and length of the septa and change in the shape of the chambers. A form which is not elongated is represented by Plate 4, figure 4.

The phylogenetic relationships of *Plectogyra* in the Ste. Genevieve limestone are not clear. Undoubtedly, specimens belonging to this genus are closely related to the St. Louis forms, but they differ in several significant ways, such as the tendency to become elongated and to have much less extensive secondary deposits. The reduction of secondary deposits in the Ste. Genevieve forms cannot be ascribed to regressive evolution, however, since the height and size of the hook is greater than in any specimens from lower zones. The general character of the Ste. Genevieve endothyroids resembles that of the lower Chesteran forms more than it does those of the St. Louis. The large size of all the Ste. Genevieve specimens tends to link them with the assemblage of the Meramecian forms more than any other single feature.

Specimens of *Endothyra* are present in the rocks of the Ste. Genevieve and they show marked resemblance to the St. Louis forms. The rate of expansion of the spiral and the development of secondary deposits in both St. Louis and Ste. Genevieve shells are commonly greater. The secondary deposits consist of a single well-developed hook in the last chamber, accompanied in some specimens by evidence of partially resorbed bases in preceding chambers. The fact that the septa are more numerous in Ste. Genevieve forms tends to produce a smoother outline of the exterior surface of the shell and less swelling of the chambers between the sutures.

Various forms of *Endothyra* from the Ste. Genevieve limestone are illustrated in Plate 4, figures 3, 5, and 10. The hook-shaped secondary deposit is exceptionally well shown in Plate 4, figure 10. An enlarged view of the wall structure of a portion of the shell represented in this figure is shown in Plate 4, figure 2. This unretouched enlargement shows the nature of the junction of the septum with the wall of the next chamber. The dark outer layer is especially well shown.

In considering phylogenetic relationships of the Ste. Genevieve forms of *Endothyra*, close resemblance to the St. Louis forms except in number of chambers per volution may be noted. The Ste. Genevieve specimens are only slightly more advanced than the St. Louis forms.

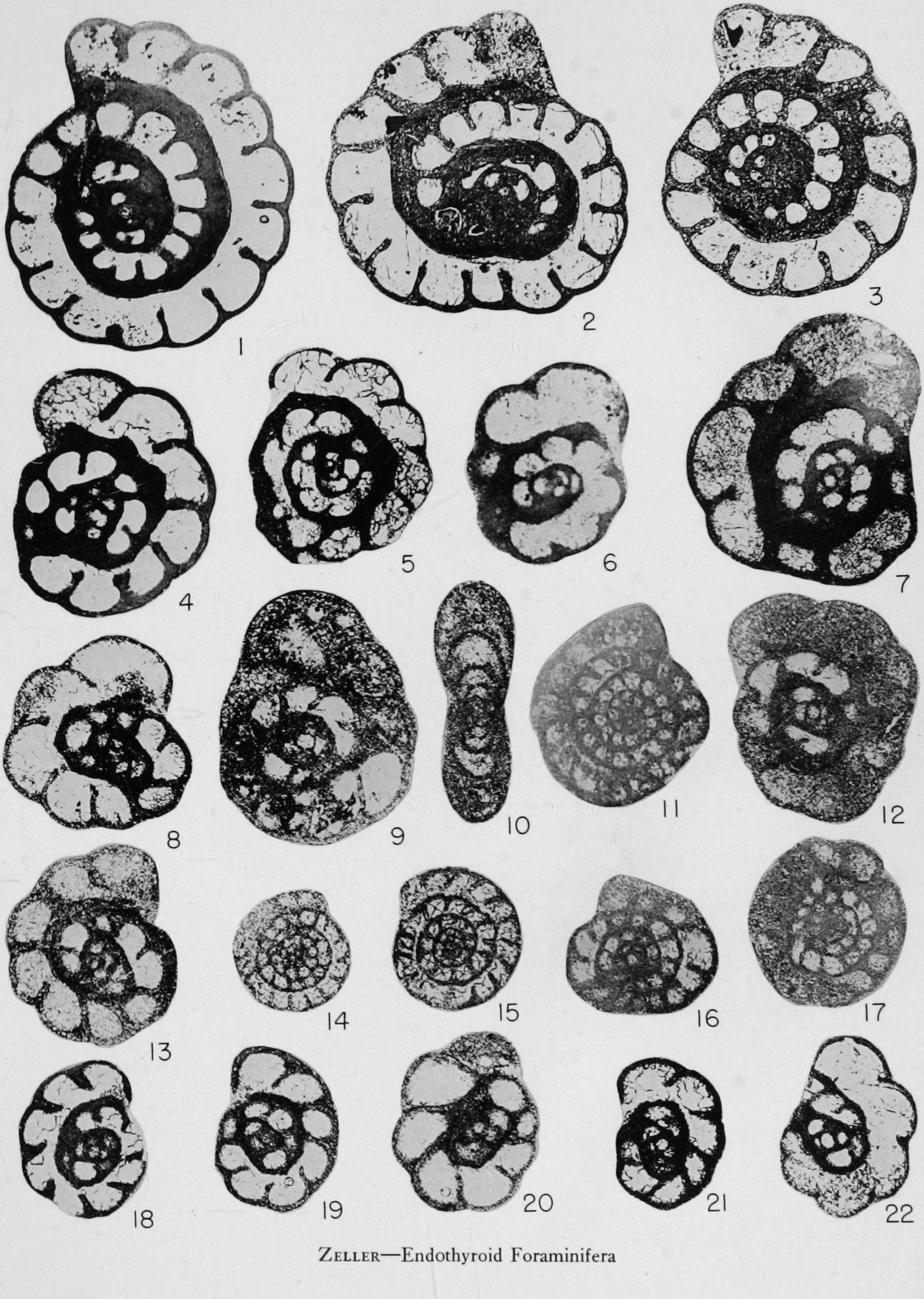
CHESTERAN FORMS

A marked difference in size between Chesteran and Meramecian forms of endothyroids makes it easy to separate these two groups. Throughout the entire Mississippian section in the type area, size is one of the most important criteria for differentiation of these foraminifers derived from successive main stratigraphic divisions. The range in size within a given division, such as Kinderhookian, Osagian, Meramecian, and Chesteran, normally is very slight. On the other hand, the size variation across boundaries of these divisions is commonly large enough to be identified as an abrupt change. The endothyroids found in Chesteran rocks, especially near the base of the section, are three to five times smaller than the largest Meramecian forms. Proceeding upward within the Chesteran

EXPLANATION OF PLATE 5

All figures $\times$ 100

Figure		Page
1, 2, 3	*Plectogyra sp.* Horizontal axial sections showing massive secondary deposit on floor of chambers; marine zone Liverpool cyclothem, Middle Pennsylvanian, Fulton County, Illinois	21
4, 7	*Plectogyra sp.* Horizontal axial sections showing secondary deposits; Kinkaid formation, Upper Mississippian (Chesteran), near Chester, Illinois	20
5	*Plectogyra sp.* Horizontal axial section showing massive secondary deposit on floor of chamber; the last one-third volution has been broken away; Ferdinand formation, Middle Pennsylvanian, Spencer County, Indiana	21
6	*Plectogyra sp.* Inclined secton showing aperture; Kinkaid formation, Upper Mississippian (Chesteran) near Chester, Illinois.	20
8	*Plectogyra sp.* Well oriented section showing thin walls; Clore formation, Upper Mississippian (Chesteran), Chester, Illinois	20
9, 12	*Plectogyra sp.* Horizontal axial sections; poorly preserved material; Vienna formation, Upper Mississippian (Chesteran), Chester, Illinois	20
10	*Millerella sp.* Saggital sections; Vienna formation, Upper Mississippian (Chesteran), Chester, Illinois	20
11, 14, 15	*Millerella sp.* Saggital sections; Vienna formation, Upper Mississippian (Chesteran), Chester, Illinois	20
13, 19	*Plectogyra sp.* Horizontal axial sections of typical forms; Glen Dean formation, Upper Mississippian (Chesteran), Chester, Illinois.	19
16, 17	*Millerella sp.* Oblique sections; Glen Dean formation, Upper Mississippian (Chesteran), Chester, Illinois	20
18	*Plectogyra sp.* Horizontal axial section; taken from well cuttings, Glen Dean formation ?, Upper Mississippian (Chesteran).	19
20, 21	*Plectogyra sp.* Horizontal axial sections showing aperture; Paint Creek formation, Upper Mississippian (Chesteran), Modoc, Illinois.	19
22	*Plectogyra sp.* Horizontal axial section; Pennington formation, Upper Mississippian (Chesteran), Tennessee	20



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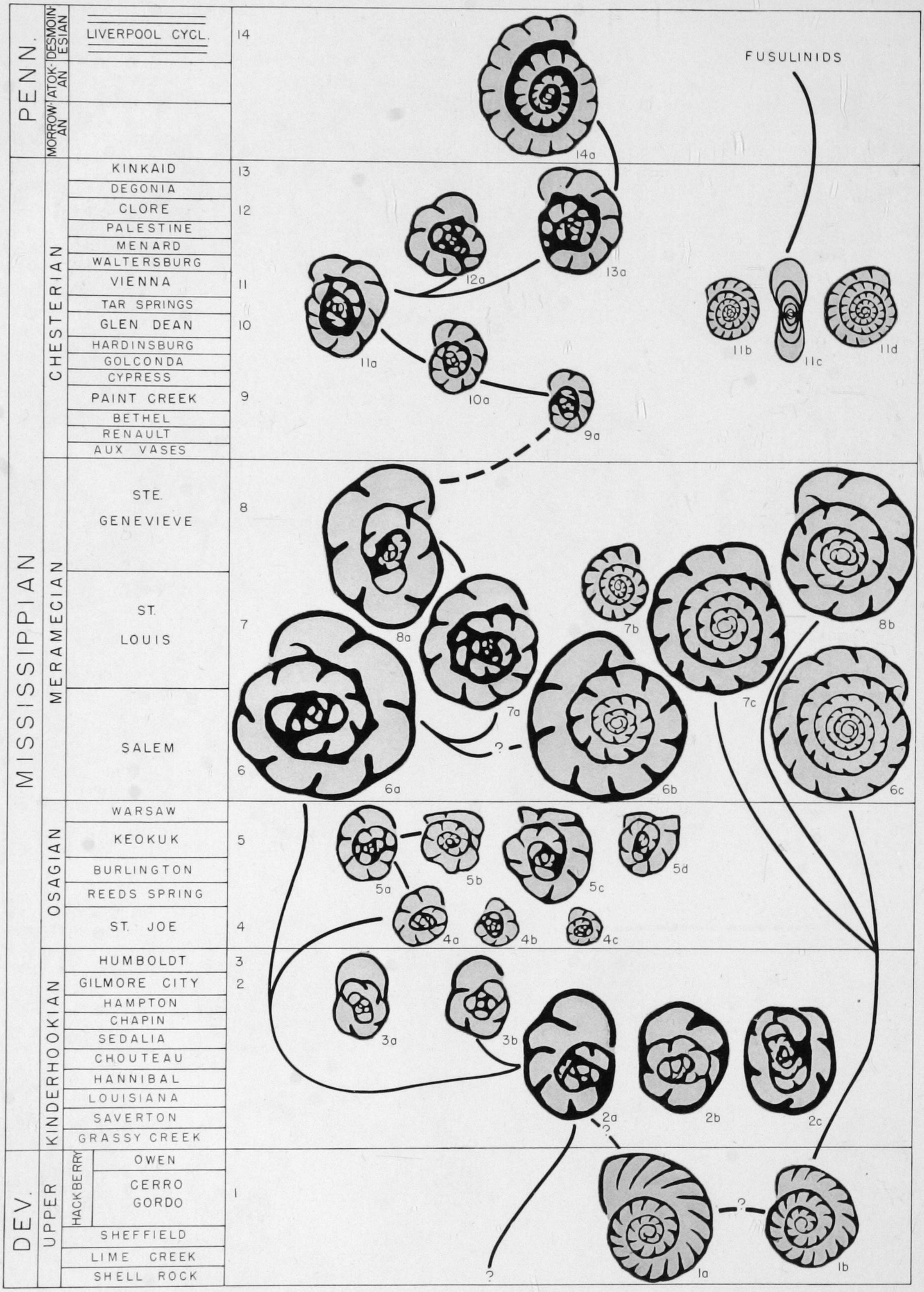

Zeller—Endothyroid Foraminifera

succession, a significant increase in the size of endothyroid shells is found to exist, the average of forms from the top of the section being about one-third larger than those from near the base.

An important paleontological feature of Chesteran rocks is the sudden appearance of the primitive fusulinid, *Millerella,* specimens of which have been obtained from both the Glen Dean and Vienna limestones. It is worthy of note that the appearance of *Millerella* and disappearance of true *Endothyra* are coincident. The resemblance of *Millerella* to *Endothyra* cannot be ignored, but differences in their shell morphology are such that it is impossible as yet to be certain that *Millerella* is the direct descendent of *Endothyra.* Despite the absence of known planispiral endothyroids in Chesteran deposits, the genus *Plectogyra* is well represented and its varying forms constitute an evolutionary sequence within this part of the Upper Mississippian section.

Plectogyra has been obtained from oölitic limestone in the Paint Creek formation (Pl. 5, figs. 20, 21) near the base of the Chesteran sequence. The specimens are elongated like many other Chesteran representatives of the genus, and they have high angles of rotation, a feature which characterizes all observed Chesteran forms of *Plectogyra.* Secondary deposits are not well shown by either of the Paint Creek specimens figured, but they are present in the form of small nodes on the inner spirothecal wall. The nodes are normally fuesd at their bases, so that a thin veneer of secondary calcite covers the floor of the chambers. Owing to elongation of the shell, the chambers vary in shape, but commonly they are swollen between the sutures.

The Glen Dean limestone has yielded both *Plectogyra* and *Millerella.* The general shape of specimens of *Plectogyra* very closely resembles shells from the Paint Creek formation but their secondary deposits are more advanced both in character and distribution in the shell. As shown by typical Glen Dean forms (Pl. 5, figs. 13, 19), the secondary deposits are extensive and the shell walls are somewhat thickened. Augmentation of secondary deposits represents a trend which continues throughout the Chesteran section into the Pennsylvanian. In the Glen Dean specimens complete fusion of the nodes has been accomplished and a layer of secondary calcite on the spirotheca is recognized through all stages of shell growth. Almost no evidence of resorption is found anywhere and the heights of the tunnel and aperture are nearly, if not exactly, the same. In some Glen Dean forms, local variations are seen in the thickness of deposits on the floor of the chambers. The thickenings occur in the same position as the nodes and are apparently the reflection of the nodes through the calcite layer deposited over and between them. A few Glen Dean shells show deposition of secondary material on the anterior side of the septa where they join the outer wall of the following chamber. Where this occurs, it gives a smooth, rounded outline to the cross section of the chamber. The location and development of this particular type of secondary deposit is extremely erratic. In some specimens none of these deposits can be found, whereas in others only certain chambers show them.

The first appearance of forms resembling *Millerella* in the Mississippian section is in the Glen Dean limestone. Specimens are not common and they are very primitive. M. L. THOMPSON (personal com-

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EXPLANATION OF PLATE 6

This plate is a diagrammatic representation of presumed phylogenetic trends of the endothyroids. Specimens which are most nearly representative of the average forms have been selected and size relationships between forms have been retained.

FIGURE	PAGE
1a, b—Endothyra gallowayi (HENBEST) variant forms from Cerro Gordo formation, Upper Devonian	21
2a, c—Plectogyra; variant forms from the Gilmore City formation, Lower Mississippian	22
3a, b—Plectogyra; different sections of similar forms from the Humboldt oölite, Lower Mississippian	22
4a, c—Plectogyra; variant forms from the St. Joe formation, Lower Mississippian	22
5a-d—Plectogyra. 5a-c, Variant forms from the Keokuk formation, Lower Mississippian; *5d,* Short Creek oölite, Lower Mississippian	22
6a-c—Plectogyra and *Endothyra* from the Salem formation, Upper Mississippian; *6a, Plectogyra; 6b, c,* variant forms of *Endothyra,*	22
7a-c—Plectogyra and *Endothyra* from the St. Louis formation, Upper Mississippian; *7a, Plectogyra plectogyra; 7b,* dwarf form of *Endothyra; 7c* normal form of *Endothyra,*	22
8a, b—Plectogyra and *Endothyra,* Ste. Genevieve formation, Upper Mississippian; *8a, Plectogyra; 8b, Endothyra.*	22
9—Plectogyra, Paint Creek formation, Upper Mississippian	22
10—Plectogyra, Glen Dean formation; Upper Mississippian	22
11a-d—Plectogyra and *Millerella?,* Vienna formation, Upper Mississippian; *11a, Plectogyra; 11b-d, Millerella*	22
12—Plectogyra, Clore formation, Upper Mississippian	22
13—Plectogyra, Kinkaid formation, Upper Mississippian	22
14—Plectogyra, Marine zone in Liverpool cyclothem, Middle Pennsylvania	22

munication) has confirmed identification of them as possibly belonging to the genus *Millerella*. The preservation of the specimens is poor and no axial sections were obtained. Accordingly, no detailed information as to the nature of secondary deposits or wall structure has been ascertained.

The Vienna limestone contains specimens of *Plectogyra*. Unforunately, their preservation is so poor that only major details of shell morphology can be observed. The forms are elongated and slightly larger than the Glen Dean specimens. They possess hooks which are fused at the base, so that a continuous thick layer is present between them. The amount of angular distortion of the spiral coil is about the same as that of the Glen Dean and Paint Creek forms. The chambers of the Vienna specimens are strongly swollen between the sutures (Pl. 5, figs. 9, 12).

The presence in the Vienna limestone of numerous, well-preserved forms which strongly resemble *Millerella* may be of stratigraphic importance. One axial section which was obtained fails to show strongly developed chomata. The shells seem to be almost completely involute and slightly umbilicate. Four to five volutions are present in the adult specimens. The tunnel is very low and seemingly has slight angular width. Sagittal sections are shown in Plate 5, figures 11, 14, and 15; one axial section is given in Plate 5, figure 10.

The Clore limestone has yielded a single specimen of *Plectogyra*. Its angular distortion seems to be very large and secondary deposits, which are well shown, consist of a prominently developed, massive hook in the final chamber and typical massive deposits on the floor of the chambers with thickening behind each of the septa. The walls of the Clore specimen are extremely thin. The septa are long and the chambers are more strongly swollen between the sutures than any other observed Chesteran forms. The less elongate appearance of the shell and a slightly more rapid expansion of the spiral seem to distinguish the Clore specimen (Pl. 5, fig. 8).

The Kinkaid limestone contains abundant specimens of *Plectogyra* which are easily distinguishable from other Chestertan forms. The Kinkaid shells are larger than any other Chesteran representatives of *Plectogyra*. The degree of rotational distortion seems to be slightly greater than in the lower Chesteran specimens, but because no perfectly oriented sections could be obtained, this is not certain. The secondary deposits are the most valuable single characteristic for differentiation of the Kinkaid specimens. Hooks or nodes are well developed, but the amount of material deposited on the inner spirothecal wall between the hooks is greatly increased over that deposited in any of the older Chesteran forms. The total thickness of the inner spirothecal wall is twice that of the original wall in the spaces between the nodes. The nodes themselves rise above the thickened wall so that total thickness of the spirotheca at the center of a node is three to four times the thickness of the original wall. No evidence of resorption, except at the free edges of the septa, is noted. The chambers are slightly swollen between the sutures. The shells of most Kinkaid specimens are somewhat elongated and part of the secondary deposit may be built out in front of the aperture before the addition of the next chamber. The apparent addition of secondary material in front of the aperture is indicated in Plate 5, figure 4. Plate 5, figure 7, shows a slightly oblique horizontal axial section of a specimen which has particularly well-developed secondary deposits. Plate 5, figure 6, is an inclined section which also shows the thickened inner spirotheca.

The phylogenetic relationships of the Chesteran forms of *Plectogyra* to forms stratigraphically older and younger are comparatively easy to interpret. Likewise, the evolutionary trends within the Chesteran succession seems to be regular progressive. The morphologic features which show the evolutionary trends of *Plectogyra* best throughout the Upper Mississippian are those of the secondary deposits. The hooks and nodes seen in Meramecian shells are obviously related directly to the thick spirothecal deposits of the Chesteran forms. The development of these deposits from their simplest and thinnest expression in Paint Creek shells to their maximum development in the Kinkaid shells is plain. The tendency of the shell to be elongated, which was first noted in upper Ste. Genevieve forms, continues through the Chesteran section. The development of increasingly high angles of rotational distortion, also, in Chesteran plectogyroids might be expected, since the forms in the Meramecian had shown this same trend.

The sudden decrease in size of specimens of *Plectogyra* in Chesteran rocks as compared with Ste. Genevieve forms is not fully understood. Possibly, this may be due to less favorable environmental conditions which existed in Chesteran time. The Chesteran deposits of the region studied are more elastic and less calcareous than those formed in Meramecian time and this probably brought about conditions which were less favorable to endothyroid foraminfers. The increase in size of *Plectogyra* during Chesteran time may have been caused by a gradual change of environment toward conditions more favorable for *Plectogyra*, or it may have resulted from adaptation of the plectogyroids to the less favorable conditions.

The appearance of *Millerella* and absence of *Endothyra* in Chesteran rocks may constitute evidence of the ancestry of primitive fusulinids, or it may be pure coincidence. If *Millerella* is descended from *Endothyra*, we need to determine at what stratigraphic level the wall of *Endothyra* becomes punctate and the aperture is lost. Also, there is need to ascertain the first appearance of secondary deposits which can be called chomata and whether chomata ever occur in specimens which could be classed as

Endothyra. Whether a sharp line of demarcation separates *Endothyra* and *Millerella* or transitional forms connect them remains to be determined. It is possible that study of the type region in England from which *Endothyra* was originally described may reveal the fact that *Endothyra* and *Millerella* are synonymous.

PENNSYLVANIAN FORMS

Thus far, the genus *Plectogyra* has been found to be the only representative of endothyroid foraminifers in rocks of Pennsylvanian age. As in the Chesteran, no adequate reason can be found to explain the absence of *Endothyra.* Specimens have been obtained from only two zones in the Pennsylvanian sections. These specimens were taken from the Ferdinand limestone of lower Atokan age in Indiana and the limestone member of the Liverpool cyclothem of middle Desmoinsian age in Illinois. The difference between the forms of *Plectogyra* in the upper Chesteran and those in the Pennsylvanian are not of major importance. The unconformity between the Osagian and Meramecian and the unconformity between the Meramecian and Chesteran, as represented by differences in the endothyroids, are much more definitely marked than is that between Chesteran and Pennsylvanian forms.

The one specimen from the Ferdinand limestone (Pl. 5, fig. 5) is so similar to the Kinkaid plectogyroids that critical examination is necessary to determine any basis for distinction between them. The Ferdinand specimen has smaller chambers, much thinner walls, slightly shorter septa, and a greater septal count per volution. The secondary deposits of the Ferdinand form show marked similarity to those of Kinkaid specimens, but the size of the nodes in the Pennsylvanian shell is reduced so that the deposit on the floor of the chambers is nearly the same thickness throughout. The rate of expansion of the spiral of the Ferdinand form may be slightly smaller than that of the Kinkaid forms, and the amount of rotational distortion is definitely less than in any of the Chesteran specimens.

Three well preserved specimens were obtained from the marine zone of the Liverpool cyclothem (Pl. 5, figs. 1-3). These specimens were free and could be examined before they were sectioned. They are discoidal and almost completely evolute, so that the variation in the coiling planes can be seen. Internally, the chambers of the Liverpool forms are much smaller in proportion to size of the shell than in the Ferdinand specimen. The septa are more numerous per volution and they are formed in such a manner that they curve away from the outer wall at an angle of nearly 90 degrees. In this respect, the septal orientation is very similar to that of the fusulinids. The difference in the attitude of the septa of the Liverpool forms is so marked that they could not be confused with any of the older varieties. The amount of rotational distortion in the Liverpool forms is similar to that of the Ferdinand specimen and is, therefore, considerably less than the rotational distortion of any Chesteran form. The tunnel is enlarged by resorption, but this seems to be the only portion of the shell affected. The presence of a single, massive layer of secondary calcite on the floor of the chambers is characteristic of all specimens from the Liverpool zone. Almost no variation in thickness and no definite or well defined nodes are seen in any of the specimens. The total thickness of the secondary deposits on the inner spirothecal wall is at least three times the thickness of the original wall. The deposits extend throughout the entire shell and into the juvenarium. The specimens from the Liverpool zone show deposits of secondary calcite on both the anterior and posterior sides of the free edge of the septa, giving them a bulbous appearance in cross section. The form shown in Plate 5, figure 1, is the most correctly oriented section and the specimen in figure 3 of this plate shows excellent wall structure. The comparative size of these specimens in relation to all of the other forms in the Chesteran is shown on Plate 5. The increase in size is notable and is persistent at least within the group of specimens from the Liverpool.

The Pennsylvanian forms apparently represent the continuation of phylogenetic trends established in Chesteran time. As a result of the comparatively small number of observed specimens in the Pennsylvanian rocks, trends cannot be determined adequately. The character and distribution of secondary deposits of the forms are similar and the tendency to develop a shell having more and smaller chambers is noted in both. The attitude of the septa in the higher Pennsylvanian form is distinctly different from the lower one, but whether this indicates an evolutionary trend is uncertain. The increase in size of the forms in the higher Pennsylvanian zone may denote a trend.

SUMMARY OF PHYLOGENETIC TRENDS

A main purpose of this report has been to determine the degree to which the endothyroids, as designated herein, may be useful as zone markers. In order to show more clearly the trends in their development, a chart (Plate 6) has been prepared to show the character and variations in their form in relation to stratigraphic occurrence. The true size relationships of the forms illustrated are indicated.

The variant forms occurring in the Cerro Gordo beds of the Late Devonian age are shown in Plate 6, figures 1a and 1b. Which of these forms is the most primitive is uncertain. Figures 2a, 2b, and 2c indicate the variants found in the Gilmore City formation of late Kinderhookian age. The least common of the three forms (fig. 2a) has a spiral which is similar in many respects to that of the Devonian specimen shown in figure 1a and they may be related. The Gilmore City forms may have been derived from *Glomospira*, however. The various forms of *Plectogyra* in the Gilmore City are judged to have given rise to all other forms of this genus in the section, either directly or indirectly. Figures 3a and 3b are different sections of forms from the Humboldt oölite. They are smaller than the Gilmore City shells but retain general characteristics of the typical Kinderhookian types of *Plectogyra*.

Figures 4a, 4b, and 4c (Plate 6) show variation in form and size of specimens from the St. Joe formation, which are the smallest found anywhere in the section. Judged to be direct descendants of the St. Joe forms are plectogyroids of the Keokuk. Figure 5a shows the only undistorted specimen found in the upper part of the Osagian section. Figures 5b and 5c are typical of forms which show the collapsed final chambers. Figure 5d shows a specimen from the Short Creek oölite of Keokuk age in which the collapse of the final chambers also is seen. The Keokuk forms are the oldest having secondary deposits in any form.

The sudden change in character of the endothyroid fauna at the beginning of Meramecian time is evident in the chart. The differences in size of the forms above and below the Osagian-Meramecian boundary is particularly striking. Figures 6a, 6b, and 6c (Plate 6) represent the various forms of genera present in the Salem limestone. Figure 6a shows a typical shell belonging to the genus *Plectogyra* and figure 6b illustrates the rapidly expanding form of *Endothyra* which occurs throughout the Salem. The phylogenetic relationships of this particular form are uncertain, but the character of the spiral is so similar to that of the Salem *Plectogyra* that it is tentatively linked with it. Figure 6c shows the general character of the tightly coiled form, which is more or less restricted to the upper part of the section. It may be descended directly from the tightly coiled Devonian form. The character and distribution of the secondary deposits of all Salem shells is shown.

Shells from the St. Louis limestone are illustrated in figures 7a, 7b, and 7c (Plate 6.) Figure 7a shows the holotype of *Plectogyra plectogyra*. Figures 7b and 7c represent specimens of *Endothyra*, figure 7b being the dwarf form found in the lower part of the St. Louis. The restricted development of secondary deposits in the St. Louis forms of *Endothyra* is illustrated. Two specimens (figures 8a and 8b) are typical of *Plectogyra* and *Endothyra* in the Ste. Genevieve limestone, figure 8a showing well-developed secondary deposits and a somewat elongate shell form, and figure 8b illustrating hooks which are commonly better developed in the Ste. Genevieve specimens of *Endothyra* than in the St. Louis forms.

Figure 9a (Plate 6) is representative of the specimens of *Plectogyra* from the Paint Creek formation. The small size, general shell shape, and character of secondary deposits all serve to distinguish Chesteran forms from those of Meramecian age. The Paint Creek types probably are derived from those in the Ste. Genevieve. Figure 10a shows the Glen Dean form which has increased deposits of secondary calcite on the floor of the chambers. Figure 11a indicates the structure of the Vienna form of *Plectogyra*. Here, also, a significant increase in the thickness of the secondary deposits is noted. Figures 11b, 11c, and 11d, represent the genus *Millerella* as it appears in the Vienna formation. The phylogenetic relationships of *Millerella* are too indefinite to permit connecting it with the endothyroids, but resemblances may be significant. Figure 12a shows a specimen from the Clore limestone which does not fit perfectly into the evolutionary sequence of endothyroids but shows enlargement of the secondary deposits. Figure 13a is a typical form of *Plectogyra* from the Kinkaid limestone. The specimens in upper Chesteran beds are larger than those in lower zones, the largest being found in the Kinkaid. The specimen shown in figure 13a shows the maximum development of secondary deposits seen in any of the Chesteran shells. The specimen of Pennsylvanian age shown in figure 14a represents the most advanced form studied. It bears resemblances to the fusulinids in that the septa are given off at nearly right angles to the outer spiral wall, which may constitute evidence of relationship between endothyroids and fusulinids. Parallel evolution also exists between the two groups. The secondary deposits are especially noteworthy in the Liverpool specimen because they link it directly with the upper Chesteran endothyroids.

CONCLUSIONS

Endothyroids have found their greatest past usefulness in stratigraphic work on subsurface samples. They should continue to have value since they are large enough to be recognized in examination of well cuttings and yet small enough to survive the grinding effect of the drill. Another characteristic which makes endothyroids valuable in subsurface work is the fact that they are commonly associated with oölitic limestones which are readily recognized in the samples. Often, chips of oölitic limestone can be picked out of the samples for making polished sections which may show enough endothyroids to permit identification of the zone. Fossils from subsurface samples often have advantage over those from the outcrop in that they are unweathered and shells are commonly better preserved. With a complete sequence of endothyroids from a given stratigraphic section in hand, there should be no difficulty in making short range correlations on the basis of these fossils. Before long range correlation can be deemed reliable, accurate knowledge of the phylogeny of the endothyroids is necessary. Geographic distribution may influence the stratigraphic appearance of certain forms and may be responsible for prominent gaps which appear in parts of local sections.

Endothyroids have a recorded distribution which is almost world-wide. Specimens examined, although not all used in writing this report, have come from many parts of the United States, Canada, and Belgium, and it seems reasonable to expect them in Mississippian rocks throughout the world. A survey of the prospective stratigraphic usefulness of the endothyroids indicates that, with further study, this group of foraminifers may become as valuable zone markers of Mississippian deposits as the fusulinids now are in many Pennsylvanian and Permian strata.

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